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RELATIONSHIPS OF THE FAMILY ALLAGECRINIDAE, WITH DESCRIPTION OF NEW SPECIES FROM PENNSYLVANIAN ROCKS OF OKLAHOMA AND MISSOURI

RAYMOND C. MOORE

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INTRODUCTION

The family Allagecrinidae was proposed by Carpenter and Etheridge (1881)[1] to include a single new genus of crinoids, *Allagecrinus*, which they had discovered in the upper part of Lower Carboniferous beds of Scotland. The dorsal cup of this crinoid is formed of two circlets of plates, comprising obscurely divided basals that bear the large round impression of a somewhat tapering stem, and five slightly unequal, dissimilar radials. The summits of the radial plates are marked by facets for articulation of the arms. In mature cups there are two or more facets on some radials but only a single facet on others. One of the specimens studied by Carpenter and Etheridge has the lower portions of the arms attached to the dorsal cup and shows that these appendages were composed of slender cylindrical segments, uniserially arranged, and to the height of the third primibrachs, without sign of branching. The largest specimens of *Allagecrinus austinii*, the genotype species, are less than 5

[1] References to previous publications are made in this paper by citation of the name of the author and date of the publication. Titles are given in a bibliography at the end of this paper.

millimeters in greatest width and height (see fig. 1). Associated with them are dorsal cups, ten times more numerous, that are only 1 millimeter or less in greatest diameter. These very

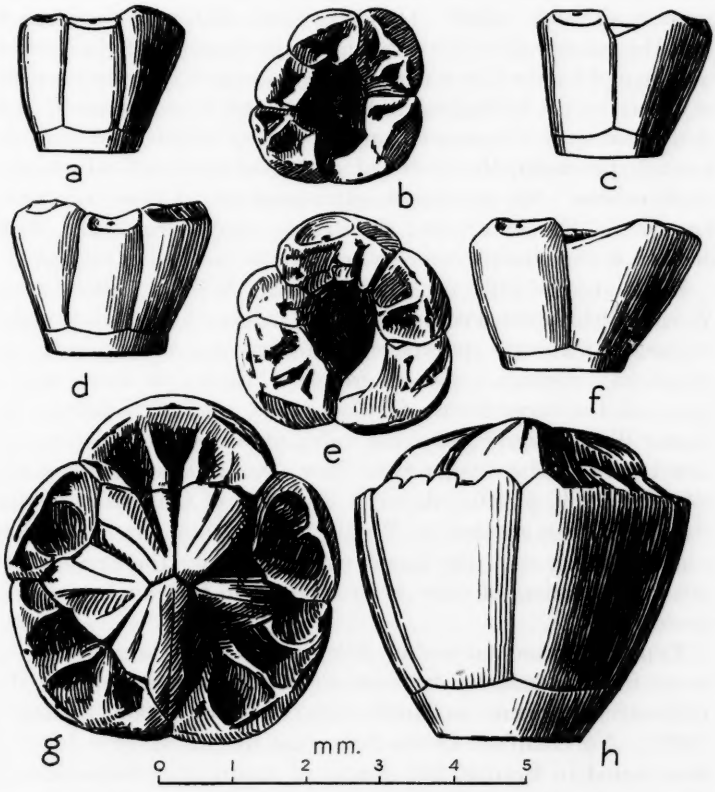

FIG. 1.—Drawings of the genotype species of *Allagecrinus* Carpenter and Etheridge and *Wrightocrinus*, n. gen. *a–c*, Left anterior ventral, and posterior views of a dorsal cup of *Allagecrinus austinii* Carpenter and Etheridge, bearing seven arm facets, specimen from upper part of Lower Carboniferous, Invertiel, Scotland, collected by James Wright; Univ. Missouri no. 6742 (camera lucida drawing). *d–f*, Similar views of another specimen having eight arm facets, from the same lot. *g–h*, Ventral and posterior views of the holotype specimen of *Wrightocrinus jakovlevi* (Wanner), from the Permian of Timor (after Wanner).

minute crinoids are also composed of a low circlet of basals and five radial plates, but unlike all but a few of the large specimens, they bear five oral plates and have a regularly symmetrical form. Most specimens show only a single small facet at the summit of each radial. Carpenter and Etheridge concluded that the microscopic cups were immature examples of the species represented by the larger cups. They assumed that the number of facets on an individual radial increased during growth and that because of a weakened union between radials and orals in mature specimens, the circlet of orals was observed only in the small calices. No crinoids closely resembling *Allagecrinus* were known to Carpenter and Etheridge, and accordingly they deemed it expedient to erect a new family to receive this genus.

Later studies (Wanner, 1929; J. M. Weller, 1930; James Wright, 1933, 1939; Peck, 1936) have indicated that most of the supposed immature specimens of *Allagecrinus* belong really to generically distinct types of crinoids. Eighty or more specimens of the large form of *Allagecrinus austinii*, collected by James Wright, agree in having radial plates of unequal size, the larger ones bearing two or even three arm facets at their summit (Wright, 1939, p. 49). About a thousand of the small crinoids that have been studied by Wright, fail to show gradation that connects them with the larger cups, either by the presence of intermediate sizes of cups or by increase in the number of arm facets.

Typical representatives of *Allagecrinus* have been found to occur fairly commonly in some Pennsylvanian deposits of the midcontinent region in North America (Kirk, 1936; Strimple, 1938). No complete crown belonging to *Allagecrinus* has yet been found in Europe, but dozens of American specimens show all the arms in position above the dorsal cup. These fossils establish the fact that none of the arms of *Allagecrinus* is branched. The arms appear on some radials earlier than on others (Kirk, 1936, p. 164), and in at least some species the primary arms are distinctly larger than the secondary ones. Also, as many as six arms may be borne by a single radial plate, although certain of the radials invariably bear only one arm.

The asymmetry of the radial plates and the peculiarity of having two or more unbranched arms attached to a single radial plate are characters that are not restricted to *Allagecrinus*. They are seen also in the genus *Catillocrinus* Shumard, which occurs in lower Mississippian rocks, and they occur in several related genera—*Mycocrinus* Schultze (Middle Devonian), *Eucatillocrinus* Springer (upper Mississippian), *Allocatillocrinus* Wanner (upper Mississippian and lower Pennsylvanian), *Paracatillocrinus* Wanner (Permian), *Neocatillocrinus* Wanner (Permian), *Isocatillocrinus* Wanner (Permian) and *Xenocatillocrinus* Wanner (Permian). All of these are referred to the family Catillocrinidae Wachsmuth and Springer (Bassler, 1938, p. 17). Wanner (1929, p. 13) has noted some of the similarities in structure of *Allagecrinus* and the Haplocrinidae, Pisocrinidae and Catillocrinidae but their possible relationships are not discussed in any detail. It is strange that in spite of the several distinctive resemblances that set allagecrinids and catillocrinids apart from most other crinoids, seemingly no student has compared them critically, nor considered the possibility of their close affinities. This may be due in part to the fact that the Allagecrinidae have been assigned to one suborder (Larviformia) of the Inadunata, and the Catillocrinidae have been placed in another suborder (Fistulata). Probably a stronger reason for failure to consider the significance of correspondences in structure is the very incomplete knowledge until recent years of the characters of *Allagecrinus* and the obscuring influence of the symmetrical or nearly symmetrical microcrinoids that were long believed to belong to *Allagecrinus*. The actuality of a close relationship has been emphasized by study of numerous small crinoids from the Morrow rocks of northeastern Oklahoma. These show growth stages of a species of *Allocatillocrinus* in which immature specimens are indistinguishable from *Allagecrinus*.

This paper reviews the characters of crinoids that have been assigned to the Allagecrinidae and Catillocrinidae, and on the basis of inferred genetic relationships, undertakes reclassification of them. The catillocrinids are transferred to the family Allagecrinidae and the conclusion is advanced that Wachsmuth and

Springer's suborders Larviformia and Fistulata lack validity. The evolution of the Allagecrinidae is discussed.

Previous work.—Subsequent to the description of *Allagecrinus austinii* by Carpenter and Etheridge in 1881, already noted, only two species were referred to this genus in more than 40 years. These were *A. carpenteri* Wachsmuth (1882) from Chester beds (upper Mississippian) of Illinois and Alabama, and *A. americanus* Rowley (1895), from the Louisiana limestone (lower Mississippian) of Missouri. The former was accepted by Wachsmuth and Springer (1886, p. 165) and Wanner (1924, p. 309) as belonging to *Allagecrinus*, but was assigned to *Catillocrinus* by Springer (1923, p. 26). Later, it was designated as genotype of *Allocatillocrinus* by Wanner (1937, p. 111). In 1924, Wanner (p. 308) described a Permian crinoid from Timor that was identified as belonging to *Allagecrinus*, and in 1929 and 1930 he described nine more Permian species under this genus. Yakovlev (1927) added four species from Upper Carboniferous and Lower Permian beds of Russia, and two species have been described from Pennsylvanian rocks of Oklahoma (Kirk, 1936; Strimple, 1938). Peck (1935) contributed a study of the growth stages of *A. americanus* and description of another lower Mississippian species referred to *Allagecrinus*. Four species from Scotland, in addition to *A. austinii*, were placed in this genus by Wright (1932, 1933). All together, 24 species have been regarded as belonging to *Allagecrinus*, although several belong elsewhere.

Wanner (1929, p. 11) first announced the conclusion that the numerous specimens classed by Carpenter and Etheridge as immature individuals of *Allagecrinus austinii* belong really to some other species of this genus. It was the opinion of J. M. Weller (1930, p. 8) that these minute forms were distinct not only specifically but also generically from the so-called adult examples of *A. austinii*. Weller had found numerous Pennsylvanian microcrinoids that correspond closely to "immature" types of *Allagecrinus*, and on the basis of these American specimens, he introduced the new genus *Callimorphocrinus* (Weller, 1930, p. 15). Subsequently, Wright (1932, p. 342) reached the

conclusion that the "adult" and "immature" examples of *A. austinii*, as interpreted by Carpenter and Etheridge, really represent two or more species, and he restricted application of the name *A. austinii* to the large or "adult" specimens. In the following year, Wright (1933, p. 206) accepted Weller's genus *Callimorphocrinus* as applicable to the symmetrical microscopic forms having an oral circlet. From Scottish localities Wright gathered many hundred specimens of *Callimorphocrinus* that he assigned to two species (*C. scoticus*, *C. elongatus*) and he distinguished two new species of *Allagecrinus*, as redefined (*a. garpelensis*, *A. biplex*). All of Wright's specimens that are referred to *Allagecrinus*, except a few supposed immature examples, show a total of six or more arm facets on the summit of the radials. Detached radials, each having four, five, and even six arm-bearing facets, were found by Wright (1939, p. 50). The discovery of numerous complete crowns of *Allagecrinus* (Kirk, 1936; Strimple, 1938) in Pennsylvanian rocks of northeastern Oklahoma shows that the arms are relatively long, slender, and unbranched, exactly as in *Catillocrinus*.

The occurrence of crinoids called *Catillocrinus* in Lower Carboniferous rocks of Tennessee was first reported by Troost (1850) at a meeting in 1849, but inasmuch as there was no published description or illustration, the name was a *nomen nudum* until Shumard (1866) gave it standing by publication of an adequate diagnosis. *Catillocrinus tennesseeae* was described and by monotypy is established as the genotype species. A manuscript that had been prepared by Troost, who died in 1850, was turned over to the Smithsonian Institution and, together with his collection of fossils, came into the hands of James Hall and others. Shumard's description of *Catillocrinus* is not that of Troost, and accordingly the authorship of this genus must be assigned wholly to Shumard, even though Shumard (1866, p. 358) credited the name to Troost. The manuscript of Troost remained unpublished for more than 60 years, until Wood (1909) gave it extensive annotation and emendation.

A few months after Shumard's introduction of the genus *Catillocrinus*, Meek and Worthen (1866) described a similar

crinoid from lower Mississippian rocks at Burlington, Iowa, designating it as *Synbathocrinus* (*Nematocrinus*) *wachsmuthi*.[2] They regarded *Nematocrinus* as a new subgenus or genus, but when the type specimen was illustrated and redescribed two years later (Meek and Worthen, 1868, p. 335), it was called *Catillocrinus wachsmuthi*. Another species, *Catillocrinus bradleyi*, was described by Meek and Worthen (1873, p. 504) from the Keokuk limestone of Indiana. In 1923, Springer transferred *Allagecrinus carpenteri* Wachsmuth to *Catillocrinus* and introduced two additional species, *C. turbinatus* and *C. shumardi*. All of these crinoids occur in Mississippian rocks. Recently described species assigned to *Catillocrinus* are *C. scoticus* Wright (1933, p. 194; 1939, p. 52) from the upper part of the Lower Carboniferous rocks of Scotland, and *C. morrowensis* Strimple (1940, p. 4), from lower Pennsylvanian rocks of southern Oklahoma. All together, eight species have been referred to *Catillocrinus*.

Wanner, in 1916 (p. 6), defined a genus, called *Paracatillocrinus*, that is closely related to *Catillocrinus*, and described three species from Permian rocks of Timor. In 1923, Springer, (p. 19) suggested the possible desirability of differentiating under the name *Eucatillocrinus* the type of crinoid represented by *Catillocrinus bradleyi*, and although he did not himself adopt this proposal, *Eucatillocrinus* is now recognized under Springer's authorship, and is based on the genotype (*C. bradleyi*) designated by him (Wanner, 1937, p. 111; Bassler, 1938, p. 17). In 1937, Wanner introduced four new catillocrinid genera: *Allocatillocrinus*, based on *Catillocrinus carpenteri* as genotype, *Neocatillocrinus*, *Xenocatillocrinus*, and *Isocatillocrinus*, each of the last three being represented by a new species from the Permian of Timor. *Catillocrinus scoticus* Wright was referred by Wanner (p. 111) to *Allocatillocrinus*.

[2] Judging from imprint dates given with Shumard's paper, it was published in sections dated August, 1865, to February, 1866. The part dealing with *Catillocrinus* seems to have been printed in August, 1865, but it does not follow that this part was distributed in 1865. Copies of the completed publication were issued in March, 1866 (St. Louis Acad. Sci., Trans., vol. 2, p. 555, 1868), and this antedates the appearance of Meek and Worthen's paper describing *Nematocrinus*, which bears the imprint of July, 1866.

The family assignments to be made for *Allagecrinus, Catillocrinus* and their allies have been studied by several paleontologists, including especially Wachsmuth and Springer (1886), Bather (1900), Springer (1913, 1923), Jaekel (1918), and Wanner (1929, 1937). *Allagecrinus* was referred to the Haplocrinidae by Wachsmuth and Springer (1886, p. 158), but the Allagecrinidae have been recognized as a family by De Loriol (1882), Bather (1900), Springer (1913), Jaekel (1918), Wanner (1924, 1929, 1930), Yakovlev (1927), Kirk (1930, 1936), Weller (1930), Wright (1932, 1933, 1939), Peck (1935, 1936), Strimple (1938), and Bassler (1938). In addition to *Allagecrinus*, the following genera are currently (see Bassler, 1938, p. 16) assigned to the Allagecrinidae: *Hybochilocrinus* J. M. Weller (1930), *Callimorphocrinus* J. M. Weller (1930), and *Trophocrinus* Kirk (1930). The genus *Aidemocrinus* J. M. Weller (1930, p. 28) was referred by him tentatively to the Allagecrinidae but is assigned by Bassler (1938, p. 22) to the Hypocrinidae. *Catillocrinus* was assigned to the Pisocrinidae by Zittel (1879) and De Loriol (1882), but after Wachsmuth and Springer (1886, p. 267) proposed the family Catillocrinidae, which originally comprised the two genera *Catillocrinus* and *Mycocrinus*, most authors (Bather, 1900; Springer, 1913, 1923; Jaekel, 1918; Wanner, 1916, 1937; Bassler, 1938) have accepted this classification. The following genera are currently assigned to the Catillocrinidae: *Catillocrinus* Shumard (1866), *Mycocrinus* Schultze (1866), *Eucatillocrinus* Springer (1923), *Paracatillocrinus* Wanner (1916), *Allocatillocrinus* Wanner (1937), *Isocatillocrinus* Wanner (1937), *Neocatillocrinus* Wanner (1937) and *Xenocatillocrinus* Wanner (1937).

CHARACTERS OF ALLAGECRINUS

It is desirable to review briefly but systematically the known morphologic characters of *Allagecrinus*, as this genus is now understood, excluding species that are referable to *Callimorphocrinus* and others that do not conform closely to the structure of *A. austinii*. Data supplied by Wright (1932, 1933, 1939) based on re-study of the types and on numerous additional specimens permit authoritative reference to the genotype species.

Also, through the kindness of Raymond E. Peck, of the University of Missouri, in loaning specimens, I have had opportunity to study well preserved examples of *A. austinii*, collected by Wright. Supplemental information of importance is reliably drawn from American Upper Carboniferous specimens, which agree entirely with the Scottish types in structural features.

Dorsal Cup

The dorsal cup of *Allagecrinus* is sub-circular, pentalobate or stelliform in outline, when viewed from the ventral or dorsal side. The height may be approximately equal to the greatest width, but more commonly it is smaller and may be as little as one half the width. The dorsal cups are small. The largest observed cup among Scottish specimens has a height of about 5 mm and a slightly greater width; the largest cup among American specimens has a height of about 5 mm and a width of 10 mm.

The cup is composed of two circlets of plates, basals and radials (see figs. 1, 9, 12, 13). Although the presence of five BB[3] has been reported (Wachsmuth and Springer, 1866, p. 164; Springer, 1913, p. 209), this is erroneous, for there are no authentic observations of more than three of these plates,—one small one and two large ones (Wright, 1939, p. 48). In many examples it is difficult or impossible to determine the location of sutures between the BB plates, and there is evidently a tendency toward fusion of the elements of this circlet. The position of the small B is seemingly not constant, but it tends to occur most commonly in the posterior interradius. The diameter of the basal circlet is generally one half or more than half that of the cup, and it may be almost equal to that of the cup. Owing to the large size of the proximal columnal, however, only a small distal area of each plate appears outside of the stem impression. In some specimens the distal part of the BB circlet is sub-vertical but in others it is nearly horizontal.

The upper part of the cup of *Allagecrinus* is composed of five

[3] Plates of the calyx of crinoids are commonly designated by abbreviations that have become customary. They are explained in previous papers (Moore and Plummer, 1938; Moore, 1939).

unequal RR. One that is identified as the laR is invariably a little smaller, or in some cases very distinctly smaller, than the others, and this plate is uniformly characterized by the presence of only one arm facet. Other RR, likewise, may have only a single facet, but these plates are somewhat wider, and in most specimens two or three of the RR bear more than one facet. The rpR is commonly identifiable by its slightly sloping left shoulder and by a notch that this produces at the summit of the cup. This corresponds in position to a reduction in thickness of the plate so as to form a clearly marked indentation of the otherwise rounded outline of the body cavity of the cup. The right-hand part of the summit of this plate (rpR) bears a single arm facet except in the case of *Allagecrinus jakovlevi* Wanner (1929, p. 15) and *A. biplex* Wright (1932, p. 348). The left shoulder of the rpR may have the appearance of an arm facet, showing a faint articular ridge and a distinct dorsal canal, as in the case of normal facets, but it seems that this merely represents the place of articulation of the first tube plate of the anal series, as demonstrated by Wright (1932, pp. 341–347). Carpenter and Etheridge did not recognize the existence of an anal series and mistook the ossicle above the left side of the rpR for an arm segment.

The lpR is almost invariably a multifaceted plate in specimens of *Allagecrinus*, and it may bear as many as six arm facets. Commonly, the aR or raR, or both, also bear more than a single arm facet. In *A. biplex* Wright (1932, p. 348), the rpR contains two arm facets in addition to the place of articulation of the anal plate. This plate most commonly contains three facets in *A. jakovlevi* Wanner (1929, p. 17) but the number is reported to range from one to five; the multifaceted nature of the rpR and absence of an anal series in this species seem to indicate that it is generically distinct from *Allagecrinus*. *A. multibrachiatus* Yakovlev has a single facet on the laR and seems to bear only one arm facet adjoining the place of articulation of the anal plate on the lpR (Yakovlev, 1927, pl. 6, fig. 8). In reporting the occurrence of five facets on each R, 25 in all, for this species, Wanner (1929, p. 18) is clearly in error, as shown

by examination of Yakovlev's illustration and by his statements in the Russian text, which do not bear out the misleading abbreviated diagnosis in the author's summary in French; Wanner (1929, p. 4), also states that *A. multibrachiatus* has 15 arms.

Each of the arm facets of the RR in *Allagecrinus* is characterized by the presence of a strong transverse ridge that separates an arcuate depressed area on the outer or dorsal side from a much larger, elongate depression on the inner or ventral side of the facetal area. The opening of a rounded canal is located centrally on the outer slope of the transverse ridge, and where the surface is weathered, the canal opening seems to interrupt the ridge. Contiguous facets on any one of the RR are divided by a strong ridge that terminates abruptly a little short of the position of the transverse ridges of the facet. In all specimens observed by me, the crests of the ridges and the general plane of the summit of the RR slope slightly inward. This is the case in the Scottish specimens, although the part of the facet outside the transverse ridge slopes outward.

A significant feature that is much more evident in some specimens than others is an inequality in height of the different RR, and combined with this, there is evidence of lateral encroachment of the summit portions of certain plates on adjoining ones. These inequalities are not distributed in a random manner. The laR tends to be a trifle lower than the adjoining lpR and aR, the angles of which encroach slightly but distinctly upon the laR. Similarly, an encroachment and overlap of the upper left margin of the aR on the raR, and of the upper left margin of the raR on the rpR may be observed in specimens of *Allagecrinus*. These features, along with other strongly accented characters, are points of correspondence with *Catillocrinus* and allied genera.

Arms

The arms of *Allagecrinus* are tall, slender, unbranched structures, consisting of uniserially arranged segments that are flattened, rounded, or somewhat angulated on the external side. The ventral side bears a deep narrow food groove. There are

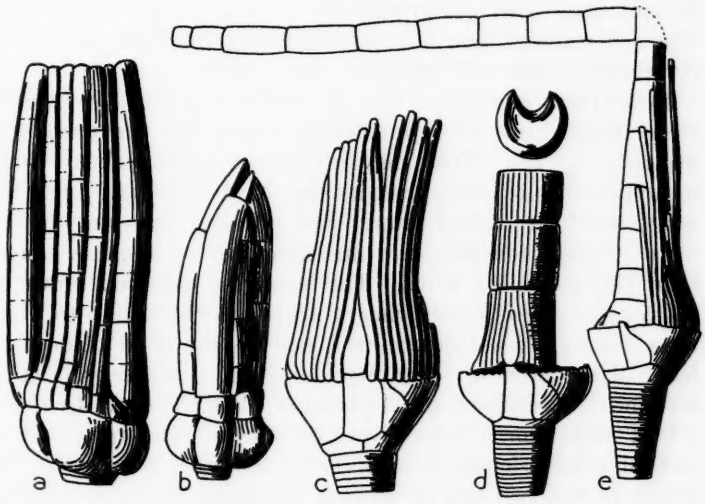

FIG. 2.—Drawings of crowns or calices and part of attached stem representing *Allagecrinus, Catillocrinus* and *Eucatillocrinus.*

a, Allagecrinus bassleri Strimple, a well preserved crown showing the large arms attached to the laR and rpR, base of the anal series on the left shoulder of the rpR, and the slender arms of the lpR; from the upper Ochelata group (Stanton horizon), Missouri stage, Pennsylvanian, at Bartlesville, Okla., (× 4.5), (after Strimple).

b, Allagecrinus strimplei Kirk, an adult specimen with five arms; a primary arm (?left anterior) in center of view, from the Drum (Dewey) limestone, Missouri stage, Pennsylvanian, at Dewey, Okla., (× 4.5), (after Kirk).

c, Catillocrinus turbinatus Springer, a nearly complete crown showing the slender arms and prominent anal plate attached to the raised left shoulder of the rpR; from the New Providence shale, Osage stage, Mississippian, at Button Mould Knob, Ky., (× 2.2), (after Springer).

d, Catillocrinus tennesseeae Shumard, posterior view of a specimen having part of the stem and the lower three segments of a massive anal tube crescentic in cross section and bearing imprints of the slender arms; the raised process on the rpR bears an anal plate that is attached to the tube; New Providence shale at Button Mould Knob, (× 1.6), (after Springer).

e, Eucatillocrinus bradleyi (Meek and Worthen), a specimen showing a long, almost complete anal tube that rises from the rpR (at left edge of view of the cup); the proximally enlarged stem and several of the slender arms are also shown; Keokuk limestone, Osage stage, Mississippian, at Crawfordsville, Ind., (× 2.1), (after Springer).

no pinnules. The first primibrach of each arm is a short quadrangular segment, and the next following brachials are almost invariably longer and generally more slender.

Kirk (1936) has shown that in *A. strimplei* Kirk five moderately robust arms of approximately equal size are present at maturity (fig. 2*b*). These may be differentiated as primary arms, for appearance of these precedes that of the slender, thread-like arms, which are added later. The primary arms are thicker, more strongly rounded, and are composed of longer segments than the secondary arms. The youngest observed crown of *A. strimplei* shows three primary arms, but the radials to which these belong are not determined, nor has the order of development of the arms of the different rays in this species been ascertained. Specimens of *A. bassleri* Strimple show two very robust arms, borne respectively by the laR and rpR, and six to twelve very slender arms borne by the other three RR. The length of the two sets of arms is the same, six to seven times the height of the dorsal cup. The arms rise vertically from the cup in closely apposed position. Wright (1933, p. 203) has observed immature specimens of *A. austinii* having arm facets only on the rpR, laR and raR, and he has noted that following the three-armed stage an arm is developed on the lpR and lastly on the aR. As described subsequently in this paper, the order of appearance of arm facets in *Allagecrinus pecki*, n. sp., is first on the rpR and then in sequence on the laR, raR, lpR and aR. This corresponds to the order of arm development in other microcrinoids, such as *Callimorphocrinus*, *Hybochilocrinus* and *Trophocrinus*, so far as this is known (see Peck, 1935, p. 768; 1936, pp. 285–287).

The general structure, arrangement, and appearance of the arms of *Allagecrinus* correspond to those of catillocrinid genera, among which, also, there is evidence of difference in the size of the arms in some species.

Anal tube

The anal tube of *Allagecrinus* has essentially the form of an arm, and it is probably in fact a modified arm structure. The

posterior interradius was not recognized by Carpenter and Etheridge in their study of the genotype species. It was identified by Wright (1932, p. 343), however, who observed that the facet on the left shoulder of the rpR is marked by a canal and ridge that are closer to the outside lip of the R than in the case of the other facets; the plate, presumably the lowest of the anal series, which appears above the left shoulder of the rpR, is thinner than the lBr of the normal arms, and it is more evenly hollowed on the inner side, not being marked by a narrow groove in the manner of the Br. The lower part of the anal series can be seen in the beautifully preserved type specimen of *A. bassleri* Strimple, which I have had opportunity to examine (fig. 2*a*). The lowest anal plate resembles the first primibrach of one of the small arms, and the tube closely resembles the adjoining arms. The correctness of identification of the posterior interradius and of the interpretation of anal structures is confirmed by Wright's (1932, p. 342) discovery of the presence of the oral arch in one of the syntypes of *A. austinii* and in other Scottish specimens. The posterior oral is distinguished by its shape and relation to the other plates, and by the presence of an opening that is interpreted as the anal vent.

Oral plates

An arch consisting of five small oral plates, resting on the inner margin of the radial summits, has been observed in several specimens of *Allagecrinus*, including one of the syntypes of *A. austinii*. In most cases, however, these plates are not preserved, and they are not seen in any mature American specimen that seems to be properly assignable to this genus, although they may be present in immature specimens. According to observations by Wright (1932, p. 347), the posterior oral is slightly larger than the other four, and it differs in outline. Its proximal edge adjoins the anal series, whereas the five primary arms of the rays adjoin the grooves between the orals (see fig. 11*o*). A hydropore on the posterior oral has not been observed in Scottish specimens, but is reported in examples from Timor studied by

Wanner (1929). The latter probably do not belong to *Allagecrinus*, however.

Stem

The stem of *Allagecrinus* is round and relatively thick, and the proximal part is typically somewhat strongly tapering. The largest columnal is attached to the base of the dorsal cup, and below this segment the columnals decrease regularly in size for some distance. A distinct longitudinal curvature in the proximal portion of the stem seems to be characteristic of some species. In numerous figured examples from Scotland, the length of the individual columnals is fairly uniform and it amounts to about one sixth or more of the diameter of the columnal. The longitudinal curvature of the surface of the columnals gives the stem an annulated appearance.

A stem fragment inferred to belong to *A. strimplei* (Kirk, 1936, p. 165), consists of very thin columnals at one end, where also there is a noticeable increase in diameter; this presumably is the proximal part of the stem. Some of the other stem segments have a length equal to the width or exceeding it.

The articular faces of the columnals lack well marked crenellae, but there is commonly a somewhat raised and granulated or tuberculated area surrounding the lumen, which is small and circular in outline.

Distribution

The two dozen species that have been assigned to *Allagecrinus* are described from rocks ranging in age from basal Carboniferous to Permian. Most of these species are now definitely assigned to other genera, as indicated in the following tabulation, which shows also geographic and geologic distribution.

Species that have been referred to Allagecrinus

Lower Carboniferous

Allagecrinus austinii Carpenter and Etheridge (1881), Lower Limestone series, Scotland.

Allagecrinus garpelensis Wright (1932), Lower Limestone series, Scotland.

Callimorphocrinus elongatus (Wright) (1932), Lower Limestone series, Scotland.

Callimorphocrinus scoticus (Wright) (1932), Lower Limestone series, Scotland.
Callimorphocrinus scoticus var. *contractus* (Wright) (1932), Lower Limestone series, Scotland.
Wrightocrinus biplex (Wright) (1932), Lower Limestone series, Scotland.
Hybochilocrinus americanus (Rowley) (1895), Louisiana limestone, Kinderhook (lower Mississippian), Missouri.
Hybochilocrinus rowleyi (Peck) (1936), Louisiana limestone, Kinderhook (lower Mississippian), Missouri.
Allocatillocrinus carpenteri (Wachsmuth) (1882), Chester (upper Mississippian), Illinois and Alabama.

Upper Carboniferous

Allagecrinus strimplei Kirk (1936), Dewey (Drum) limestone, Missouri stage (upper Pennsylvanian), Oklahoma.
Allagecrinus bassleri Strimple (1938), Stanton limestone, Missouri stage (upper Pennsylvanian), Oklahoma.
Allagecrinus donetzensis Yakovlev (1927), Donetz basin, U. S. S. R.

Permian

Allagecrinus multibrachiatus Yakovlev (1927), Urals, U. S. S. R.
Allagecrinus dux Wanner (1930), Timor.
Allagecrinus inflatus Wanner (1929), Timor.
Callimorphocrinus uralensis (Yakovlev) (1927), Urals, U. S. S. R.
Callimorphocrinus uralensis var. *nodocarinatus* (Yakovlev) (1927), Urals, U. S. S. R.
Callimorphocrinus acutus (Wanner) (1929), Timor.
Callimorphocrinus excavatus (Wanner) (1929), Timor.
Callimorphocrinus indoaustralicus (Wanner) (1924), Timor.
Callimorphocrinus ornatus (Wanner) (1929), Timor.
Callimorphocrinus procerus (Wanner) (1929), Timor.
Callimorphocrinus quinquebrachiatus (Wanner) (1929), Timor.
Callimorphocrinus quinquelobus (Wanner) (1929), Timor.
Wrightocrinus jakovlevi (Wanner) (1929), Timor.

Restricting attention to species that are regarded as congeneric with *A. austinii*, it is noted that the range of *Allagecrinus* extends from the upper part of the Lower Carboniferous to the Permian. The genus is recognized in Europe, North America, and Timor.

OTHER MICROCRINOIDS THAT HAVE BEEN REFERRED TO THE ALLAGECRINIDAE

Very diminutive crinoids that have maximum height or diameter of the calyx less than 2 mm occur abundantly in some Carboniferous strata. Permian rocks of Timor, Russia, and North America have yielded numerous microcrinoids that are only a little larger. Many specimens are less than 1 mm in

longest dimension. The almost invariable presence of a circlet of oral plates, inconspicuousness or absence of arm facets, and a generally well developed pentamerous symmetery characterize these fossils. Most of the genera that are recognized in this group have been classed as belonging to the Hypocrinidae, which are distinguished, among various features, by narrow horseshoe-shaped arm facets. Four genera, besides *Allagecrinus*, have been referred to the family Allagecrinidae. These are *Callimorphocrinus* J. M. Weller (1930, p. 15), *Hybochilocrinus* J. M. Weller (1930, p. 13), *Aidemocrinus* J. M. Weller (1930, p. 28), and *Trophocrinus* Kirk (1930). It is needful to review briefly the nature of these forms.

Characters of Callimorphocrinus

Based on *Callimorphocrinus astrus* J. M. Weller,[4] from lower Pennsylvanian beds of Indiana, as genotype, this genus is de-

[4] The correct nomenclatural treatment of Weller's genus and genotype offers sundry problems. As published, the name of the genus was *Kallimorphocrinus* and it was stated that this term was derived from the Greek *kallimorphos*, meaning beautifully formed. Article 19 of the Rules of Zoological Nomenclature provides that the original orthography of a name is to be preserved unless an error of transcription (transliteration), slip of the pen, or typographical error is evident. Correct transliteration of the Greek kappa should be "C", and because the intention of the author in compounding this generic name is clear, it seems that error was made in the transcription of the root word. Certainly it is pointless to appeal to recommendations accompanying Article 8 to the effect that generic names may be formed by an arbitrary combination of letters. Accordingly, it seems proper to write *Callimorphocrinus*.

Weller (1930, p. 15) designated the genotype of this genus as "*Kallimorphocrinus astrus typicus* J. M. Weller, n. sp., n. var." Two other "varieties" of *Callimorphocrinus astrus* were described, respectively called *intermedius* and *pyramidalis*. The Rules do not recognize varieties or make provision for their nomenclature, although it is common enough practice among paleontologists to designate varieties. Moreover, the usage of paleontologists seems generally to differ from that of zoologists, a majority of whom recognize differentiation both of subspecies and varieties in some instances. A few paleontologists attempt to define mutations (in the sense of Waagen, not de Vries), but most of the students of fossils who undertake to differentiate "varieties" of species seem to be dealing with subordinate classificatory units that the Rules would denominate as subspecies. There is no inherent reason for making any distinction between mutation, as this term was just used, and subspecies. The Rules provide that "specific and subspecific names are subject to the same rules and recommendations, and from a nomenclatural standpoint they are coordinate, that is, they are of the

fined to include larviform microcrinoids of nearly perfect pentamerous symmetry having a low disc of anchylosed basals, five approximately equal radials, and a circlet of orals (see fig. 3 *a*, *b*). There is no anal plate or facet indicating the place of attachment of an anal series. The calyx is oriented readily, however, on the basis of the orals, for the posterior oral is slightly larger than the others, different from them in outline, and commonly it bears a small tubercle that marks the position of a hydropore. Kirk (1937, p. 111) has called attention to the constancy in features of the oral circlet and use of it in correct orientation of crinoid calices that lack other definitive characters.

According to Weller's descriptions and figures of species of *Callimorphocrinus*, all examples of this crinoid bear a single small arm facet at the summit of each radial, so that the cup has five arms in all. One exception is noted (Weller, 1930, p. 22) in the case of the holotype (and seemingly only known example) of *C. infacetus* J. M. Weller, which lacks a facet on the aR, because this radial "perhaps was not arm-bearing" or "the structure has been obliterated by wear." Wright (1932, pp. 350–360; 1939, p. 51) has shown conclusively that immature examples of *Callimorphocrinus* may possess fewer than five facets. Youngest specimens have no arms. A one-armed stage is followed by a two-armed stage, and as growth proceeds the number of facets gradually increases to five, or, in the case of *C. elongatus* (Wright) (1939, p. 52), to eight. Assuming that Wright was able to orient correctly the specimens studied by him, no definite order to precedence among the radials in acquiring facets is observed.

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same value" (Art. 11). As applied to the genotype of *Callimorphocrinus*, this means that use of different specific and subspecific (or varietal) names for the most narrowly defined section of *Callimorphocrinus astrus* is incorrect. This should be designated simply as *Callimorphocrinus astrus*, as *Callimorphocrinus astrus* (sensu stricto), or as *Callimorphocrinus astrus astrus*. In other words, one of the subspecies (or varieties) must be the "original" and it cannot carry a name that is different from the specific name. An alternative treatment of Weller's three named subspecies or varieties of *C. astrus* would be to raise each of them to specific rank, designating them as *C. typicus*, *C. intermedius* and *C. pyramidalis*, but this seems not to accord with Weller's observations on their distinctness of differentiation. Therefore, in referring to the genotype of *Callimorphocrinus* it seems best to drop "*typicus*" and simply write *C. astrus*.

The articular facets of *Callimorphocrinus* are reported by Weller (1930, p. 16) to bear a strong, transverse ridge that is bordered on the outer side by a small ligament pit and by the beveled edge of the radial; on the inner side of the ridge is a groovelike concavity that bears near its middle the small opening of the axial canal. This description, as Weller notes, is based

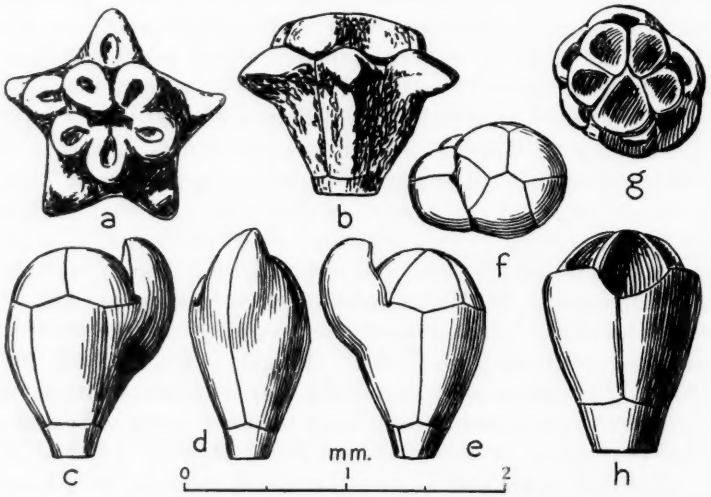

FIG. 3.—Drawings of the genotype species of *Callimorphocrinus*, *Trophocrinus*, and *Hybochilocrinus*. *a,b*, Ventral and lateral views of *Callimorphocrinus astrus* J. M. Weller, lower Pennsylvanian, Warren County, Indiana (after Weller). *c–f*, Anterior, lateral left, posterior, and ventral views of *Trophocrinus tumidus* Kirk, Welden limestone, lower Mississippian, near Ada, Okla. (after Kirk). *g,h*, Ventral and posterior views of *Hybochilocrinus americanus* (Rowley), from the Louisiana limestone, lower Mississippian, Louisiana, Mo. (after Weller and Peck).

mostly on *C. pocillus* J. M. Weller, rather than on the genotype species, which has very narrow facets that do not show a distinct transverse ridge or ligament pit. The significance of this in determining diagnostic features of *Callimorphocrinus* lies in the possibility, if not probability, that *C. pocillus* is based on an immature specimen—only the holotype is mentioned—of a species of *Allagecrinus*. Concerning the Scottish species, Wright

(1932, p. 351) states only that the facets "apparently are of the same general plan as those of *Allagecrinus austinii*." The facets of examples of *Callimorphocrinus* that I have had opportunity to study are narrow rounded depressions, like those of *C. astrus*, lacking a distinct ridge or other markings.

The validity of distinction between *Callimorphocrinus* and *Allagecrinus* is established on a number of grounds. The rpR is differentiated at an early stage in the latter genus but this plate is not distinguishable even in mature representatives of the former except by reference to characters of the orals. An anal series is absent in *Callimorphocrinus* but present in *Allagecrinus*. The dorsal cup is regularly symmetrical in the one genus but more or less distinctly asymmetrical in the other. The number of facets on a mature cup of *Callimorphocrinus* is normally five, whereas fully developed specimens of *Allagecrinus* commonly have six or more facets. The arms of *Callimorphocrinus* are presumably unbranched and probably rather short. They are composed of uniserial segments, as shown by specimens having the first brachials in some rays (Wanner, 1929; Wright, 1932). The occurrence of more than five facets on a few examples of *Callimorphocrinus elongatus* marks a trend in the direction of *Allagecrinus* but this variation does not introduce uncertainty in the generic and specific identification. Cups belonging to *Allagecrinus* that have only five or fewer arm facets tend to approach *Callimorphocrinus* in their characters and some specimens may be difficult to distinguish certainly. There is rarely reason for question, however, if numerous specimens are available for study. Representatives of the two genera may occur together or not. At Scottish localities, for example, *Callimorphocrinus* and *Allagecrinus* are found associated in the same beds but in many places only one of the two forms has been observed.

Callimorphocrinus ranges from the lower part of the Lower Carboniferous into the Permian, and species assigned to it have been described from North America, Scotland, Russia, and Timor. In the following list, species that in my judgment may prove to belong to a genus other than *Callimorphocrinus* are indicated by a query (?).

Species assigned to Callimorphocrinus

Lower Carboniferous

Callimorphocrinus pristinus Peck (1936), Fern Glen, Osage (lower Mississippian), Missouri.

Callimorphocrinus puteatus Peck (1936), Fern Glen, Osage (lower Mississippian), Missouri.

Callimorphocrinus scoticus (Wright) (1932), Lower Limestone series, Scotland.

Callimorphocrinus scoticus var. *contractus* (Wright) (1932), Lower Limestone series, Scotland.

Callimorphocrinus elongatus (Wright) (1932), Lower Limestone series, Scotland.

Upper Carboniferous

Callimorphocrinus astrus J. M. Weller (1930), Des Moines stage (lower Pennsylvanian), Indiana.

Callimorphocrinus astrus var. *intermedius* J. M. Weller (1930), Des Moines stage (lower Pennsylvanian), Indiana.

Callimorphocrinus astrus var. *pyramidalis* J. M. Weller (1930), Des Moines stage (lower Pennsylvanian), Indiana.

Callimorphocrinus piasaensis J. M. Weller (1930), shale below Piasa limestone (Pawnee), Des Moines stage (lower Pennsylvanian), Illinois.

Callimorphocrinus lilius J. M. Weller (1930), shale below Piasa limestone (Pawnee), Des Moines stage (lower Pennsylvanian), Missouri.

Callimorphocrinus indianensis J. M. Weller (1930), Des Moines stage (lower Pennsylvanian), Indiana.

Callimorphocrinus vanpelti J. M. Weller (1930), shale below Piasa limestone (Pawnee), Des Moines stage (lower Pennsylvanian), Illinois.

Callimorphocrinus infacetus J. M. Weller (1930), Des Moines stage (lower Pennsylvanian), Indiana.

(?)*Callimorphocrinus pocillus* J. M. Weller (1930), Des Moines stage (lower Pennsylvanian), Indiana. (?Young *Allagecrinus*).

(?)*Callimorphocrinus illinoisensis* J. M. Weller (1930), shale below Piasa limestone (Pawnee), Des Moines stage (lower Pennsylvanian), Illinois. (?Young *Allagecrinus*).

Callimorphocrinus knighti J. M. Weller (1930), Des Moines stage (lower Pennsylvanian), Missouri.

Callimorphocrinus expansus J. M. Weller (1930), shale below Piasa limestone (Pawnee), Des Moines stage (lower Pennsylvanian), Illinois.

Permian

Callimorphocrinus uralensis (Yakovlev) (1927), Urals, U. S. S. R.

Callimorphocrinus uralensis var. *nodocarinatus* (Yakovlev) (1927), Urals, U. S. S. R.

Callimorphocrinus acutus (Wanner) (1929), Timor.

Callimorphocrinus indoaustralicus (Wanner) (1929), Timor.

Callimorphocrinus procerus (Wanner) (1929), Timor.

Callimorphocrinus quinquelobus (Wanner) (1929), Timor.

(?)*Callimorphocrinus excavatus* (Wanner) (1929), Timor.

(?)*Callimorphocrinus ornatus* (Wanner) (1929), Timor.

(?)*Callimorphocrinus quinquebrachiatus* (Wanner) (1929), Timor.

Characters of Hybochilocrinus

The genus *Hybochilocrinus* was introduced by J. M. Weller (1930, p. 13) to include a single species called *Allagecrinus americanus* Rowley (1895, p. 219). This species occurs in the Louisiana limestone of northeastern Missouri, which is regarded by Branson (1938, p. 5) as Upper Devonian, but assigned by most geologists to the basal part of the Mississippian. Specimens are abundant. About 100 calices were contained in the lot studied by Weller, and Peck (1935, p. 766) records the finding of more than 300 specimens in two small samples of the clay parting between beds of the limestone.

The calices of *H. americanus* are very small, having an average height of about 1.3 mm and a width half as great (see fig. 3 *g*, *h*). The round stem impression is large and the sides of the cup are steep. The basal circlet seems to consist of three plates, but this is uncertain, for sutures are not seen. The five radials have nearly equal widths in young specimens but in mature individuals the laR is distinctly narrower than the other plates and the two posterior RR are widest. The cup is only slightly asymmetrical in form, however. The left shoulder of the rpR is strongly beveled, forming a notch that holds a moderately large anal plate, essentially as in *Allagecrinus austinii*. Arm facets consist of small suboval or rectangular depressions, surrounded by a thin lip that is formed by direct upward extension of the surface of the radial. There is no transverse ridge and in the depression of the facets only a very narrow brachial opening may be noted as a feature. Peck (1935, p. 766) observes that smallest examples of this crinoid are armless, and that facets first appear on the rpR and laR, somewhat later on the raR and lpR, and lastly on the aR. Specimens retaining the lowest brachials in place show that the arms are uniserial, but their height is unknown; doubtless they are unbranched. A subhemispherical oral circlet rises above the radials. The orals have raised borders and thus appear concave. The posterior oral is longer and wider than the others and near its center bears a short tubercle that probably represents the position of a hydropore.

It is somewhat strange that Weller submits no discussion of the relationships of *Hybochilocrinus* and *Allagecrinus*. He merely states that "because its peculiarities sharply differentiate it from all other known crinoids, the new genus *Hybochilocrinus* is introduced" for the reception of *Allagecrinus americanus*. Seemingly, Weller was impressed by the presence in *A. americanus* of a prominent circlet of orals, not known in "adult" specimens of *Allagecrinus austinii* described by Carpenter and Etheridge, and by the occurrence of no more than five arm facets on the Louisiana limestone microcrinoids. Wright (1932, p. 342) subsequently reported discovery of the presence of orals in one of Carpenter and Etheridge's "adult" types and in other specimens of *A. austinii*, and he expressed the judgment (Wright, 1933, p. 204) that *Hybochilocrinus* should be regarded as a synonym of *Allagecrinus*. Peck (1935, 1936), likewise, does not recognize Weller's genus, though no reasons are given. Bassler (1938, pp. 16, 114) treats *Hybochilocrinus* as a valid genus. It is apparent that the chief distinction, if not the only one of significance, between *Hybochilocrinus* and *Allagecrinus* is in the character of the arm facets. None of the radial plates of *Hybochilocrinus* bears more than a single facet and each such facet is evidently a simpler structure than in *Allagecrinus*. This distinction, supplemented by the considerably smaller dimensions of abundant adult examples of *Hybochilocrinus*, seems to afford sufficient ground for acceptance. The presence of a tubercle (?hydropore) on the posterior oral of *Hybochilocrinus* and absence of a similar structure in *Allagecrinus* (see Wright, 1932, p. 346) is probably not an important difference.

Only one species, besides the genotype, is referable to *Hybochilocrinus*. This is *H. rowleyi* (Peck) (1936, p. 284) from the Chouteau limestone lower Mississippian, of Missouri.

Characters of Trophocrinus

Trophocrinus is a peculiarly aberrant microcrinoid that is distinguished by an upward hoodlike projection of the radial plates on the left side of the calyx. The lpR and laR are involved almost equally in forming this structure, which is interpreted

(Kirk, 1930, p. 210) as a brood pouch (fig. 3 *c–f*). Only one of the radials of the genotype species, *T. tumidus* Kirk, is seen to bear an arm facet; that is the laR, the facet being located at the lower edge of the brood pouch. A subhemispherical crown of oral plates surmounts the RR. The posterior oral is pentagonal in outline, longer and wider than the others, and bears a hydropore tubercle.

Trophocrinus tumidus, represented by two known specimens, occurs in the Weldon limestone (called Sycamore limestone by Kirk, 1930, p. 212), lower Mississippian, near Ada, Okla. One additional species assigned to this genus has been described. It is *T. exsertus* Peck (1936, p. 285), from the Chouteau limestone, lower Mississippian, Boone County, Missouri.

Characters of Aidemocrinus

A half dozen tiny crinoids, about 0.5 mm high were set apart in 1930 by Weller (p. 28) as representing a new genus and species. They were called *Aidemocrinus odiosus*. The calices consist of a low basal disc, five equal radials, and a convex circlet of orals. All the specimens are armless.

A. odiosus is much smaller than most of the crinoids found associated with it but, as noted by Weller, it is very similar to some of them in form and structural features except the arm facets. It resembles both *Callimorphocrinus indianensis* and *Dichostreblocrinus scrobiculus* obtained from the same horizon and locality. Weller concluded that the specimens called *A. odiosus* were not early growth stages of one of these other crinoids because he did not find intermediate connecting forms. He tentatively referred *Aidemocrinus* to the Allagecrinidae, but Bassler (1938, pp. 22, 36) lists it, along with *Dichostreblocrinus*, among the Hypocrinidae. Despite the observation that the few examples of *A. odiosus* studied by Weller seem not to be joined by intermediate stages with *Callimorphocrinus* or *Dichostreblocrinus*, there is every reason to judge that *Aidemocrinus* is founded on extremely immature representatives of one or other of these genera, probably *Callimorphocrinus*. At least until this opinion is demonstrated to be incorrect, *Aidemocrinus* should be regarded

as without standing. I regard it as a synonym of *Callimorphocrinus*.

The small lot of specimens that constitutes the only published record for recognition of *Aidemocrinus odiosus* came from the same lower Pennsylvanian horizon and Indiana locality that yielded *Callimorphocrinus indianensis* and several other microcrinoids described by Weller.

CHARACTERS OF CATILLOCRINUS

For the purpose of comparisons with *Allagecrinus*, it is desirable first to examine characters of the genus *Catillocrinus*, and then to make note of distinguishing features of other genera that have been classed as belonging to the family Catillocrinidae.

Catillocrinus was established in 1866 on the basis of *Catillocrinus tennesseeae* Shumard, as has been noted previously (see fig. 2*d*). This species occurs in the New Providence shale, Kinderhook (lower Mississippian), of Kentucky and Tennessee. It is represented in the Springer collection at the U. S. National Museum by the type specimen and about 30 additional well-preserved dorsal cups and crowns. Because several species that formerly were assigned to *Catillocrinus* are now placed elsewhere, the following summary of the characters of this genus is based mainly on Springer's (1923) study of the genotype species, supplemented by my own examination of the type and other specimens in the U. S. National Museum.

Dorsal Cup

The cup of *Catillocrinus* is sub-circular or faintly elliptical in outline, as viewed from above or below. The relatively broad base is flat or gently concave, and the straight or evenly curved sides slope steeply upward to the slightly uneven summit line of the RR. The height of the cup is one half or less than half the greatest width. The cup of *C. tennesseeae* is characterized by its relatively large size, the diameter of some specimens being as great as 25 mm. (see fig. 4).

Catillocrinus generally has been regarded as a monocyclic crinoid (Wachsmuth and Springer, 1886, p. 269; Bather, 1900,

p. 150; Springer, 1913, p. 214). In 1923, however, Springer published a study of the family Catillocrinidae in which the conclusion was reached that the genotype of *Catillocrinus* is definitely a dicyclic form, as might be inferred from the description by Shu-

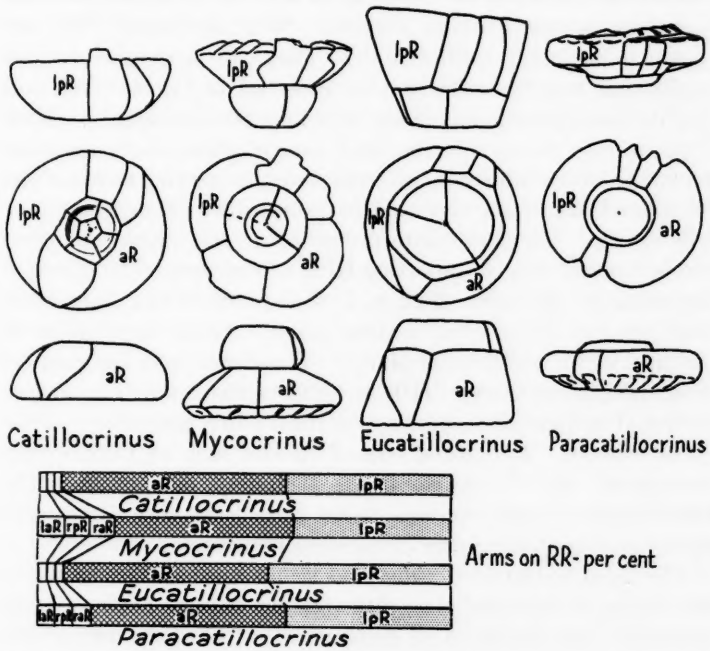

FIG. 4.—Diagrams showing the form and structure of the dorsal cup of the genotype species of *Catillocrinus*, *Mycocrinus*, *Eucatillocrinus* and *Paracatillocrinus*. This group of genera is distinguished by the very large number of arms borne by two of the radials (aR and lpR) and by an accompanying reduction in size of the other three radials. The percentage distribution of arms on the radials is indicated in the graph.

mard (1866, p. 357). The presence of infrabasals is also indicated in *C. turbinatus* Springer (1923, pp. 12, 26). The very small circlet of IBB seemingly composed of three plates, is located in the central part of the large round stem impression, and in the inside of the cup it appears as a low conical elevation, apparently

ordered in some specimens by encircling scalelike plates (see Springer, 1923, pl. 2, fig. 2). The existence of IBB is indicated clearly in Springer's discussion, in some of his figures, and by inspection of specimens in the U. S. National Museum. Nevertheless, there is room for doubt as to whether *C. tennesseeae* and *C. turbinatus* are actually dicyclic. Well developed IBB are known in no other catillocrinids. They are lacking in crinoid stocks that may be conceived as ancestral to *Catillocrinus* and they do not appear in any forms that may be descendants. Kirk (1929, p. 160) thinks that the small cone of plates above the stem lumen of *Catillocrinus* is an internal structure serving to house the chambered organ, as observed in some other crinoids, and he believes that Springer's interpretation of the plates as infrabasals is erroneous. Supporting Kirk's conclusion is the observation made by Springer (1923, p. 7) that plates of the "infrabasal ring" are "as thin as fine writing paper," which is strikingly in contrast to the thick basal plates. Therefore, until the case for recognizing occurrence of IBB in *Catillocrinus* is much more conclusive than now, it seems best to regard this genus as a monocyclic crinoid. The dorsal cup of species such as *Catillocrinus wachsmuthi* and *C. shumardi* are definitely monocyclic. The basal circlet of each contains three plates, the sutures between them meeting at the center of the stem impression.

The basal circlet of *Catillocrinus* seems normally to consist of five plates of subequal size, although the sutures between them cannot be seen clearly in all specimens. Most of the area of this circlet is covered by the large stem impression.

The RR show very striking inequality of size. There are two very large plates (aR and lpR) and three small ones. The proximal margins of the aR, lpR, and rpR are approximately equal in width, and each is nearly one half the width of the proximal sutures of the other two RR. At the summit of the cup, however, the discrepancy in width of the RR is very marked, the aR subtending about 52 percent of the circumference, the lpR about 38 percent, and the combined total for the other three RR amounting to only 10 percent. Each of the three small RR bears only a single arm facet, whereas the two large RR bear

respectively 18 to 24 (rpR) and 22 to 31 (aR) facets. The left shoulder of the rpR is distinctly elevated for contact with a large anal plate. The articular surfaces of the RR are greatly thickened, so as to make a platform that in width is one fourth to one third the diameter of the cup. The round opening of a dorsal canal is observed near the outer margin of each arm facet. The inner part of the facet consists of a long narrow groove. Except for an elongate, narrowly compressed form, the arm facets of *Catillocrinus* are entirely similar in appearance and morphology to the facets of *Allagecrinus*.

The suture between the two posterior RR is essentially straight, but other inter-RR sutures curve somewhat strongly. Moreover, there is a definite manner of encroachment of one R on its neighbor near the summit of the cup. The aR overlaps both the adjoining RR; the lpR overlaps the laR, and the raR overlaps the rpR. This peculiarity is exactly the same as in *Allagecrinus*, but it is much more accentuated in *Catillocrinus*. On the other hand, there is little observable unevenness in the height of the RR in *Catillocrinus* such as may appear in *Allagecrinus*.

Arms

The arms of *Catillocrinus* are very long slender uniserial appendages that have no bifurcations and lack pinnules (fig. 2*c*, *d*). The arms are all uniform in size and are composed of segments of approximately uniform length, which is about twice the arm width. The total number of arms in *C. tennesseeae* and *C. turbinatus* is unusually large, ranging from 37 to 58. No other crinoid genus with unbranched arms has nearly so many arms.

Anal Sac

One of the most peculiar and distinctive features of *Catillocrinus* is its long anal sac, composed of ponderous crescentic segments (see fig. 2*d*). This has been described in some detail by Springer (1923, p. 17). The diameter of the tube is approximately one half that of the dorsal cup, and the length of each segment is as great as or greater than the height of the dorsal cup. The total height of the sac is at least equal to the length of the

arms and the diameter diminishes little in the lower portion of the sac, which may be marked by longitudinal grooves made by the imprint of the arms pressed against it. The position of the sac, its broadly hollowed part directed anteriorly, and marks of ligamentous union between the segments support the conclusion that this structure is a greatly enlarged and modified arm. As in the brachial segments, there is a dorsal canal opening that is centrally located near the outer margin of the sac segments. Clearly this corresponds to the canal opening on the left shoulder of the rpR.

A peculiar elongate anal plate, which is distinct from the sac segments, rests on the protuberant portion of the rpR and interlocks with the lowest part of the sac.

No trace of an oral arch has been observed in specimens of *Catillocrinus*.

Stem

The stem of *Catillocrinus* is composed of fairly uniform thin columnals that decrease somewhat regularly in width distally (fig. 2*c*, *d*). The width of the proximal columnal is approximately one half that of the dorsal cup. The articular surfaces of the columnals lack distinct crenellae, but a granulose raised area may be observed surrounding the lumen, which is small and round. The round tapering stem of *Catillocrinus* is straight in examples figured by Springer, although forms assigned to related genera show gentle curvature of the stem near the cup.

Distribution

Narrowly defined to include only species having two exceptionally large RR, and showing characters of the anal plate and sac as observed in the genotype species, *Catillocrinus* is restricted to lower Mississippian beds, and is at present known only from localities in Kentucky, Tennessee, Indiana, and Iowa. Following is a list of species that have been referred to *Catillocrinus*.

Species that have been referred to Catillocrinus

Lower Carboniferous

Catillocrinus tennesseeae Shumard (1866), New Providence shale, Osage (lower Mississippian), Tennessee and Kentucky.

Catillocrinus turbinatus Springer (1923), New Providence shale, Osage (lower Mississippian), Tennessee and Kentucky.

Catillocrinus wachsmuthi (Meek and Worthen) (1866), Burlington limestone, Osage (lower Mississippian), Iowa.

Catillocrinus shumardi Springer (1923), Keokuk limestone, Osage (lower Mississippian), Indiana.

Eucatillocrinus bradleyi (Meek and Worthen) (1873), Keokuk limestone, Osage (lower Mississippian), Indiana.

Allocatillocrinus carpenteri (Wachsmuth) (1882), Chester (upper Mississippian), Illinois, Indiana and Alabama.

Allocatillocrinus scoticus (Wright) (1933), Lower Limestone series, Scotland. Upper Carboniferous

Allocatillocrinus morrowensis (Strimple) (1940), Wapanucka limestone, Morrow (lower Pennsylvanian), Oklahoma.

CATILLOCRINID GENERA OF THE GROUP OF CATILLOCRINUS

Several genera that have characters more or less definitely similar to those of *Catillocrinus* have been differentiated, as already noted. These may be arranged in groups that seem to have genetic significance, division being made chiefly on variation in the distribution of the multifaceted radial plates. The first group is marked by having only two large radials that bear many arms, and that is designated as the group of *Catillocrinus*. The many-faceted plates are the lpR and aR. Each of the other three RR bears only a single arm. Besides *Catillocrinus*, already discussed, the group comprises *Mycocrinus* Schultze, *Eucatillocrinus* Springer, and *Paracatillocrinus* Wanner. The second group includes catillocrinids that are characterized by the presence of three or more large multifaceted radials and may be known as the group of *Allocatillocrinus*. Genera belonging to it will be described briefly later.

Characters of Mycocrinus

Mycocrinus is distinguished by the high massive nature of the basal circlet, which constitutes half or more of the total height of the cup (fig. 4). The thick basals seem to be more or less fused, for sutures are indistinct and at most only three plates in this circlet are recognized. The large aR and rpR bear 4 to 7 and 4 to 6 arm facets, respectively, and each of the other three radials has only a single facet. The left shoulder of the rpR contains a projection that marks the point of attachment of an anal plate,

as in *Catillocrinus*. Three species of *Mycocrinus* have been described, all from Middle Devonian rocks in Germany. They are *M. boletus* Schultze, the genotype, *M. granulatus* Jaekel, and *M. conicus* Springer. The cups are small, ranging in greatest width from about 5 to 11 mm. Judging from the figures given by Springer, the large radials (aR and lpR) encroach in both directions on the adjoining smaller plates. No specimens showing the arms, anal sac, stem, or an oral arch are known.

Characters of Eucatillocrinus

The form, size, and general structure of *Eucatillocrinus* are almost the same as in *Catillocrinus*, but a distinction that Springer (1923, p. 19) and others regard as important is the absence of an upward projection on the left shoulder of the rpR, which brings the first tube plate of the anal sac directly upon the rpR at the level of the arm bases (fig. 2*e*). No anal plate of special form is present as in *Catillocrinus*. The anal sac is remarkably long and slender. The round stem shows a marked tapering in the proximal region, but the downward diminution in width of the columnals is restricted to the upper one third of the stem. Specimens that show the entire length of the column, 310 to 370 mm. in length, indicate that it tapers distally to a fine point and bears a few scattered cirri (Springer, 1923).

Eucatillocrinus is represented by a single described species, *E. bradleyi* (Meek and Worthen), which occurs in the Keokuk limestone, lower Mississippian, at Crawfordsville, Ind.

Characters of Paracatillocrinus

The genus *Paracatillocrinus*, like others of the group of *Catillocrinus*, is characterized by having two very large radials (lpR and aR), which respectively bear 5 to 9 and 6 to 11 arms (fig. 4). Each of the three small radials carries only a single arm facet. The lpR shows no indication at all of an articulation for an anal plate. Some specimens, however, show an asymmetry in the outline of the body cavity, owing to an expansion of the cavity in the position of the suture between the lpR and rpR. This is a feature observed in other catillocrinids and it doubtless indi-

cates space required for reception of the lower part of the gut. In any case, it seems to serve reliably as a means for identication of the posterior interradius. Asymmetry of the radials is emphasized by increase in width of the two large radials toward the distal margins, but the sutures between the plates of this circlet are essentially straight, without indication of overlap of the large radials on the neighboring small ones.

Paracatillocrinus is represented by three described species, *P. granulosus* Wanner, *P. spinosus* Wanner, and *P. ellipticus* Wanner, all from the Permian of Timor.

GROUP OF ALLOCATILLOCRINUS

The catillocrinids that are brought together under this designation are readily differentiated from *Catillocrinus* and closely allied genera by the presence of three or more large multifaceted radials. *Allocatillocrinus* Wanner is a typical representative of this group and is the least specialized, excepting *Allagecrinus*, which on evidence of similarities in morphology and observations of ontogeny is believed to be directly ancestral to *Allocatillocrinus*. Four genera that have been classed as catillocrinids are placed in the group. *Allocatillocrinus* has three radials (lpR, aR, raR) that each bear several facets, the other two (laR, rpR) each having a single arm facet. *Neocatillocrinus* Wanner differs from *Allocatillocrinus* chiefly, if not only, in lacking a recognized anal series attached to the rpR and in having two arm facets on this plate. *Xenocatillocrinus* Wanner has a single facet on the laR but all the other radials bear four or more facets. *Isocatillocrinus* Wanner is unique among catillocrinids in having more than one arm facet on the laR; this genus bears several facets on each of the radials and seems to lack an anal series (see fig. 5).

Characters of Allocatillocrinus

Differentiation of *Allagecrinus carpenteri* Wachsmuth (1882) as the type of a distinct genus was suggested by Springer (1923, p. 19), but no proposal of a new generic name was made by him. This was done by Wanner (1937, p. 111), who chose to call the genus *Allocatillocrinus*. He designated *Allagecrinus carpenteri*

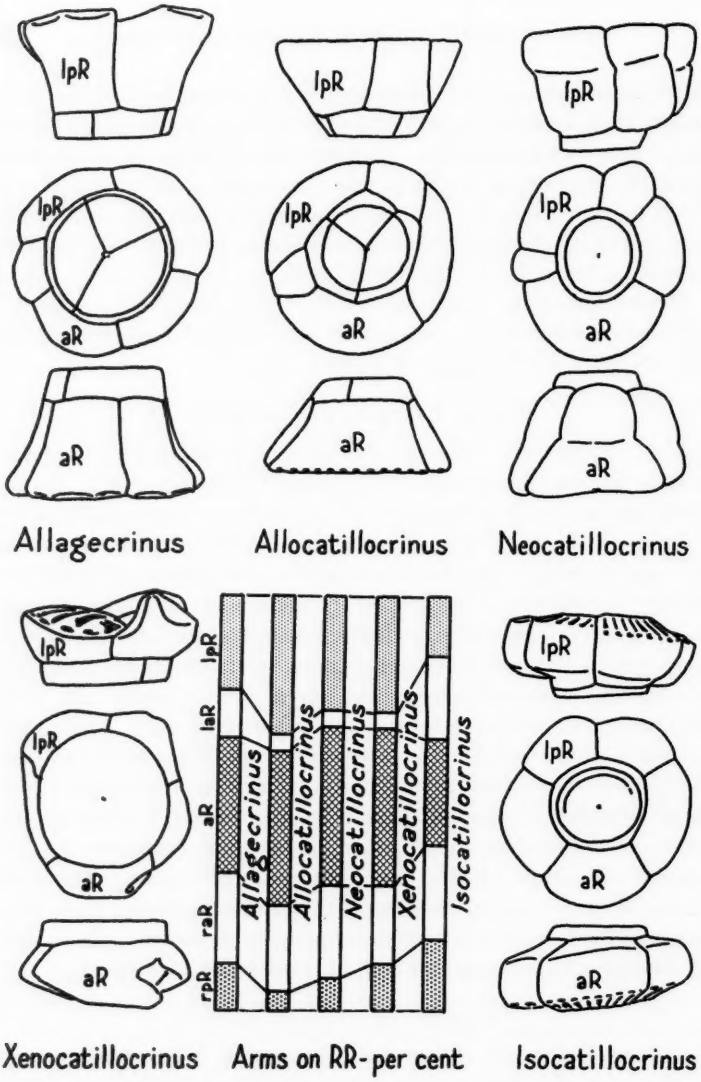

FIG. 5.—Diagrams showing the form and structure of the dorsal cup of the genotype species of *Allagecrinus, Allocatillocrinus, Neocatillocrinus, Xenocatillocrinus* and *Isocatillocrinus*. This group of genera is characterized by the relatively large number of arms borne by three of the radials (raR, aR and lpR), although this is modified in *Isocatillocrinus* (orientation altered from that of Wanner). The percentage distribution of arms on the radials is indicated in the graph.

as genotype, and at the same time referred *Catillocrinus scoticus* Wright (1933) to *Allocatillocrinus*. There is no doubt that *Catillocrinus morrowensis* Strimple (1940) and a new species here described as *Allocatillocrinus rotundus* from lower Pennsylvanian beds of Oklahoma, also belong to Wanner's genus.

The dorsal cup of *Allocatillocrinus* corresponds essentially to that of *Catillocrinus*, *Eucatillocrinus*, and others of the group. It is monocyclic, having three unequal basals that are almost covered by the proximal stem segment. The radials are markedly asymmetrical, but instead of two large plates and three small ones in this circlet, there are three large multi-armed radials and two small ones. In *Allocatillocrinus carpenteri* the number of arm facets on the lpR ranges from 5 to 8; on the aR, from 3 to 9; and on the raR, from 3 to 5. In the two syntypes of *A. scoticus*, the number of facets on these plates is respectively, 8, 11, and 7; in *A. morrowensis*, it is 9, 15, and 12; and in mature examples of *A. rotundus*, n. sp., it is 11 to 16 on the lpR, 8 to 14 on the aR, and 6 to 10 on the raR. In all the species, the laR and rpR each bear only a single arm facet, but there is evidence of articulation for an anal plate on the left shoulder of the rpR. The width of the proximal edges of the radials is nearly uniform in some examples of *Allocatillocrinus*, but in *A. carpenteri* and especially *A. scoticus* the suture at the base of the laR is distinctly narrower than the others. Lateral encroachment in definite directions of the summit portions of certain radials is visible in all specimens but it is especially striking in *A. rotundus*. The suture between the two posterior radials is straight, but all others are somewhat strongly curved, the distal part of the aR overlapping strongly on its neighbors to left and right, and the distal part of the raR and lpR projecting over the plates that adjoin them on the left. The small radials tend to be distinctly lower, as well as narrower, than the large ones. This is not very evident in *A. carpenteri*, but it produces a notched outline at the upper margin of the cup in *A. morrowensis* and is strikingly shown in *A. rotundus*. A long slender anal sac is observed in *A. carpenteri*, but this structure is not known in the case of other species. The stem is relatively long and slender, but it expands markedly near the cup.

The known occurrence of species of *Allocatillocrinus* indicates a short geologic range. It comprises the upper part of the Lower Carboniferous and lowermost part of the Upper Carboniferous. The genus occurs in Europe and North America. The following list indicates the distribution of the known species.

Species referred to Allocatillocrinus

Lower Carboniferous

Allocatillocrinus carpenteri (Wachsmuth) (1882), lower Chester (upper Mississippian), Illinois, Indiana, Alabama.

Allocatillocrinus scoticus (Wright) (1933), Lower Limestone series, Scotland.

Upper Carboniferous

Allocatillocrinus morrowensis (Strimple) (1940), Wapanucka limestone, Morrow (lower Pennsylvanian), Oklahoma.

Allocatillocrinus rotundus, n. sp., Brentwood limestone, Morrow (lower Pennsylvanian), Oklahoma.

Characters of Neocatillocrinus

As already noted, *Neocatillocrinus* seems to be entirely similar to *Allocatillocrinus*, except that there is no sign of the presence of an anal plate, and the rpR bears two arm facets (fig. 5). The rpR is proportionately not wider than in *Allocatillocrinus*, and therefore the dorsal cup is marked by three large radials and two distinctly smaller ones. *N. incissus* Wanner, the genotype and only described species, has 7 arm facets on the lpR, 10 on the aR, and 5 on the raR. Two additional specimens that have been reported recently by Marez Oyens (1940, p. 317) indicate that the total number of facets ranges from 25 to 34. The species occurs in the Permian of Timor. In size and general appearance, the dorsal cup of this crinoid is very much like some American representatives of *Allagecrinus*, but the latter have fewer arm facets and they bear marks of articulation for an anal series on the rpR.

Characters of Xenocatillocrinus

Xenocatillocrinus is defined on the basis of a single dorsal cup, named *X. wrighti* Wanner, from the Permian of Timor (fig. 5). It exhibits curiously modified shapes of the low radials, and the basals seem to be fused solidly. The laR has a single broad arm

facet, but the other plates of the radial circlet are multifaceted (lpR 8, rpR 4, raR 5, aR 10). In addition to arm facets, the rpR bears an anal series. This genus differs from *Neocatillocrinus* mainly in the shape of the cup and in characters of the rpR.

Characters of Isocatillocrinus

The genus named *Isocatillocrinus* by Wanner, from the Permian of Timor, is distinguished by the presence of several arm facets on each of the radials (fig. 5). The dorsal cup of *I. indicus*, the genotype and only known species, is very low and somewhat discoid or truncate bowl-shaped in form. The basal circlet, which is seemingly fused into a single piece, is almost entirely covered by an elliptical stem segment. The cup is relatively large, measuring about 12 to 16 mm. in greatest width. The multi-armed character of all of the radials and absence of any evidence of articulation for an anal plate gives difficulty in orientation of the cup. This problem is considered at length by Wanner (1937, p. 115) but his conclusions, tentatively drawn, fail to take account of a clearly evident bulge in the outline of the body cavity that is placed next to one of the interradial sutures. Inspection of Wanner's illustrations shows that this irregularity of the body cavity closely resembles a similar feature in *Allagecrinus* and various catillocrinids. It may be used reliably to define the posterior interradius, and it is thus indicated that the orientation given by Wanner is erroneous. He designates as laR the plate that seems really to be the aR, and so in order around the cup. A paper by Marez Oyens (1940, p. 316), which was received after preparation of this manuscript, shows that conclusions identical with those just given were reached by this author and he re-orients the specimens of *Isocatillocrinus* accordingly. A correct orientation is chiefly important in comparative study of this and related genera. Based on revised identification of the posterior interradius, the radials of the holotype of *I. indicus* bear the following number of facets: lpR 5, laR 7, aR 9, raR 8, rpR 6. Listed in the same order, example *b* of Wanner has 4, 6, 7, 6 and 5 facets, 28 in all; example *c* has 4, 7, 7, 7 and 5 facets, a total of 30.

DESCRIPTION OF WRIGHTOCRINUS, NEW GENUS

Comparative study of *Allagecrinus* and other genera that have been reviewed calls attention to divergences in structure of two species that seem to warrant recognition of them as representing a new genus. The species are *Allagecrinus jakovlevi* Wanner (1929, p. 15) (See fig. 1*g*, *h*) and *Allagecrinus biplex* Wright (1932, p. 348). These crinoids have a subpyriform calyx that is rounded-pentagonal in dorsal or ventral view. The basal circlet is a low solidly fused disc in most specimens. The radial plates are unequal, the laR and raR being narrower than the others and being distinguished further by having only one arm facet at the summit instead of two or more as in the case of the others. A low circlet of orals is present in adult stages of both species, the margin of the circlet being fixed to the inner edges of the radial summits. A small spear-shaped anal plate or pair of plates in series, appears above a notch between the posterior radials of at least one specimen of Wright's species but is absent in others, and seemingly there is no such plate in *A. jakovlevi* (fig. 1*gh*). The latter species was described on the basis of 125 complete calices that range in height from 2.9 to 6.8 mm. The Scottish species was described from 12 specimens, having a height of about 1.5 mm, but Wright (1939, p. 50) notes that since the date of his original publication he has found several more examples of this crinoid.

In 1933, Wright (pp. 201–207) reclassified the Scottish allagecrinids and considered the generic placement of all other species that he believed to belong in the Allagecrinidae. The genus *Allagecrinus* was deemed to be distinguished especially by the presence of an armlike series of anal plates, an anal opening into the calyx, and radial plates of unequal size, any of which might be multifaceted except the laR. No question as to the generic placement of *Allagecrinus biplex* seems to have been entertained by Wright at any time, and it was on the basis of this species that the rpR of *Allagecrinus* was included with other radials that may be multifaceted or axillary. This plate uniformly bears only one arm facet in species of *Allagecrinus* except *A. biplex* and *A. jakovlevi*. The latter was assigned by Wright (1933, p. 205) to *Calli-*

morphocrinus, because of its lack of an anal plate. Wanner's species, just mentioned, differs markedly from *Callimorphocrinus* in having as many as five facets on a single radial plate.

The distribution of arms on different radial plates, especially presence of more than one arm on the rpR and laR, is indicated to be one of the most significant features in generic differentiation of so-called allagecrinids and catillocrinids. The one-armed character of the plates mentioned persists in various genera while other features undergo change, and this seems to be correlated in some way with the appearance of arms on these radials at immature growth stages before other plates of the circlet acquire arms. *A. jakovlevi* and *A. biplex* indicate departures from a general rule and they exhibit similarities that support assignment of them to a separate genus. The presence or absence of anal plates, which is normally a character of generic importance, does not seem to be so in this case. It is not surprising that an anal plate or plates, present in the Lower Carboniferous species, should have disappeared in the Permian species.

The new genus is named in honor of James Wright, of Edinburgh, Scotland, who has contributed very importantly to knowledge of the rich crinoid faunas of the Lower Carboniferous rocks of Scotland, England, and Ireland. I may mention also his cordial hospitality to me on the occasion of a visit to Edinburgh in 1935 for study of the Scottish Carboniferous beds, his gifts of fossil specimens to me, and other courtesies.

Genotype.—As genotype of *Wrightocrinus* the species *Allagecrinus jakovlevi* Wanner is designated, because it is somewhat more fully described and illustrated than *A. biplex*, because it is represented by a large number of specimens, and because evolutionary characters seem to be well differentiated. To be noted incidentally is a variation in spelling of the name of this species, as given by Wanner (1929). In the description of figures the designation "*Allagecrinus Yakovlevi*" appears, but throughout the text the name is written "*Allagecrinus Jakovlevi.*" In spite of the fact that transliteration of the Russian characters composing the name of the well known paleontologist preferably and customarily results in "Yakovlev," there is no question but that

correct reference to Wanner's species must follow his orthography of the text, not that of the plate.

Occurrence.—Lower Limestone series, Scotland (*Wrightocrinus biplex*); Permian, Timor (*Wrightocrinus jakovlevi*).

RELATIONSHIPS OF ALLAGECRINUS AND CATILLOCRINID GENERA

Evidence from structural similarities

The review of characters of *Allagecrinus* and of the several catillocrinid genera that has been given calls attention to so many points of resemblance that one can hardly escape the definite conclusion that close genetic relationships exist between these crinoids. The correspondences in characters that seem to have chief significance may be summarized.

(1) *Allagecrinus* and the catillocrinids are small crinoids, most of them having a greatest diameter of the dorsal cup less than 15 mm.

(2) Probably including *Catillocrinus*, but not with entire certainty, all have monocyclic dorsal cups, in which the basal circlet is characterized by the presence of three somewhat obscurely differentiated elements or by a single fused plate (figs. 4, 5).

(3) Only the distal extremities of the basals extend beyond the margin of the proximal columnal (fig. 2).

(4) The radials of *Allagecrinus* and catillocrinid genera are asymmetrical. The degree of asymmetry varies considerably, but the pattern is the same (figs. 4, 5).

(5) All the genera under consideration possess broadly thickened summit portions of the radials that are marked by a distinctive type of arm facet, and in adult specimens one or more of the radials is multiple-armed.

(6) The facets are characterized by presence of a rounded opening of the dorsal canal near the margin of the radial summit, a more or less distinct transverse ridge, and on the side toward the body cavity by a deep narrow groove that is defined laterally by strong ridges. The general plane of the facets mostly slopes gently inward, but it may be subhorizontal or slope slightly outward.

(7) The proximal margins of the radials range from subequal to distinctly unequal. Maximum irregularity appears in the

distal part of these plates. In virtually all genera the summit portion of the aR encroaches laterally on its two neighbors, and the raR and lpR encroach to the left on their neighbors. Only in *Isocatillocrinus* does the laR fail to be characterized as a one-armed plate of more or less strongly reduced size that is partly overlapped distally by the two adjoining plates.

(8) The arms of *Allagecrinus* and of all known catillocrinids are relatively long slender appendages composed of uniserial segments. They are unbranched and bear no pinnules (fig. 2).

(9) In some species of *Allagecrinus*, arms of two sizes are observed, one of which is much more robust than the other. In *Allocatillocrinus*, three of the facets tend to be noticeably larger than the others, which implies that the arms attached to these facets are larger. Differentiation in the side of the arms is not evident in *A. carpenteri* but in other species the anterior facet of the raR and the single facets of the rpR and laR are relatively large.

It is interesting to observe that the crinoid arms composed of fused uniserial brachials, called *Stereobrachicrinus pustullosus* Mather (1915, p. 108), from Morrow beds of Arkansas and Oklahoma, correspond very closely in form to the arms of *Allagecrinus strimplei* Kirk (1936) and that specimens of *S. pustullosus* can be fitted nicely on to the large facets of *Allocatillocrinus rotundus*, n. sp., which occurs in the same Morrow beds. *Stereobrachicrinus* was defined solely on specimens of arms, and most of these are too large to fit the large facets of any discovered example of *Allocatillocrinus*, but in future it may be proved that these arms and cups belong to a single type of crinoid. In that event it will be necessary to suppress *Allocatillocrinus* (Wanner, 1937) as a synonym of *Stereobrachicrinus* (Mather, 1915). Dissociated brachial segments of slender cylindrical form that might belong to arms fitting on the smaller facets of *Allocatillocrinus* are known in the Morrow strata, but certainly none of the arms called *Stereobrachicrinus* can represent the smaller arms of *Allocatillocrinus*.

(10) Several of the catillocrinid genera are known to bear a long stout anal sac having the form of a modified arm. *Allagecrinus* has a similar but much more delicate armlike anal series. An

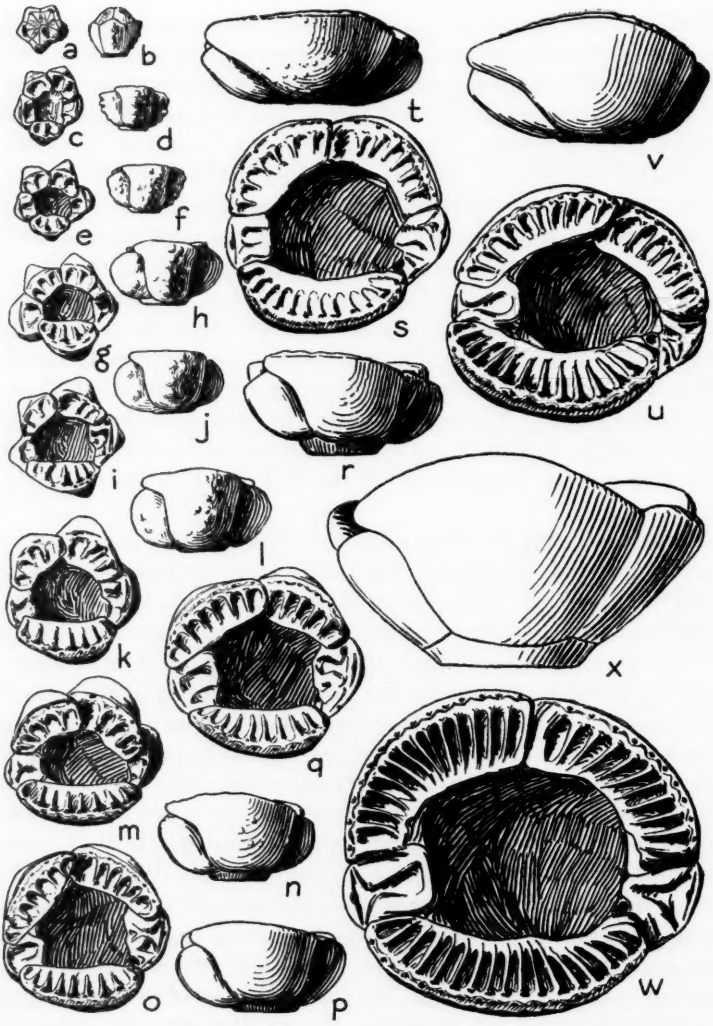

FIG. 6.—Growth series of *Allocatillocrinus rotundus*, n. sp., showing a *Callimorphocrinus*-like initial stage (*a,b*) that is somewhat doubtfully referred to this species, juvenile specimens (*c–j*) that are indistinguishable from *Allagecrinus*, and examples (*k–w*) marked by progressively increasing size that typically represent *Allocatillocrinus*. All figures × 5 and uniformly oriented with the

anal plate is present in *Allagecrinus* and several catillocrinid genera, and the mode of articulation of this plate with the left part of the rpR is deemed to have classificatory significance. Some advanced catillocrinids seem to lack an anal plate, and existence of a sac has not been demonstrated. These, like *Allagecrinus*, show a bulge in the outline of the body cavity at the posterior interradius, however.

(11) Among crinoids discussed here, and for the moment excluding *Callimorphocrinus*, *Hybochilocrinus* and *Trophocrinus*, the presence of an oral arch is known only in some examples of *Allagecrinus*.

(12) The stem of *Allagecrinus* and of catillocrinid genera, so far as known, is characterized by an expansion in width towards the base of the cup. The columnals lack well defined crenellae and are characterized by a broad, smooth or tuberculated area surrounding the small round lumen. The large size of the proximal stem segment, which covers most of the basal circlet, is a characteristic feature of *Allagecrinus* and catillocrinids.

Evidence from ontogeny of Allocatillocrinus rotundus, n. sp.

Significant evidence of the relationship of *Allagecrinus* and the genus *Allocatillocrinus* is provided by a suite of about three dozen specimens of *Allocatillocrinus rotundus*, n. sp., mostly from a single sample of Morrow shale collected in northeastern Oklahoma. These show a remarkably complete succession of growth stages ranging from very immature specimens 2.0 mm. in diameter to the maximum observed adult size having a width of 11.7 mm. (see fig. 6). The number of facets ranges from 7 to 42, increase

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lpR directed toward the observer. All specimens are from the Brentwood limestone, Morrow stage, and all but the largest specimen were obtained from outcrops at Greenleaf Lake, southeast of Braggs, Okla. Two radials (rpR, laR) of the smallest figured specimen (*a,b*) bear well defined arm facets and a third radial (raR) shows a small facet. The number of facets on the lpR, aR and raR increases with size but on the laR and rpR only one large facet is seen, although a small facet on the rpR for attachment of the anal series closely resembles that of an arm. *a,b*, no. 73853A; *c,d*, no. 73851P; *e,f*, no. 73851O; *g,h*, no. 73851M; *i,j*, no. 73851L; *k,l*, no. 73851AA; *m,n*, no. 73851AB; *o,p*, no. 738511I; *q,r*, no. 73851H; *s,t*, no. 73851R; *u,v*, no. 73851C; *w,x*, no. 451928D (from Keough quarry, 2 miles north of Fort Gibson, Okla.). All specimens classed as paratypes.

from one specimen to another forming a regular series. Features of ornamentation and shape of the dorsal cup serve also to connect the members, indicating a gradual change from somewhat strongly lobate and tubercles immature cups to rounded smooth adult cups (see figs. 6, 12). Up to a point in the series that is limited approximately by a cup diameter of 4.5 mm. and a maximum of 16 arm facets in all, the immature forms are entirely indistinguishable from *Allagecrinus*, but larger cups progressively show the typical characters of *Allocatillocrinus*. If the small specimens were found alone, they would be assigned unhesitatingly to *Allagecrinus*, and they would probably be so identified even if found associated with examples of *Allocatillocrinus*, provided intergrading forms were not seen. The evidence offered by the specimens showing growth stages of *Allocatillocrinus rotundus* points unequivocally to derivation of *Allocatillocrinus* out of *Allagecrinus*. The only essential distinction between these genera lies in the more numerous facets of the lpR, aR and raR in *Allocatillocrinus*. This brings forward the question of the dividing line between the genera, and it seems necessary to conclude that this is arbitrary. On theoretical ground such a transition between genera is expectable. Difficulties in classification and somewhat artificial definition of generic boundaries are sure to exist wherever the fossil record shows evolutionary steps between forms of life that in themselves are distinguished readily. Also, such transitions do not in any way invalidate the generic concepts, serving on the other hand to establish them in true phylogenetic relationships.

The maximum number of facets on a single radial of the cup of *Allagecrinus austinii* seems to be 3, but Wright (1939, p. 50) has collected dissociated radials having 4, 5, and in one case, 6 facets, from the beds that yield cups of this species. He identifies them as *Allagecrinus* radials, possibly belonging to *A. garpelensis* rather than *A. austinii*, however. It is very interesting that *Allocatillocrinus scoticus*, which is found in association with the allagecrinids just mentioned, has a dorsal cup that is almost identical in shape and size with these species of *Allagecrinus*, distinction being found in the much more numerous facets of the

Allocatillocrinus. The two known examples of *Allocatillocrinus scoticus* have 9 facets on the lpR, 7 on the raR, and (data lacking for one specimen)12 on the aR. It is readily thinkable that this species represents a development from little-different allagecrinids having the general character of *A. austinii*. The loose radials above mentioned are larger than corresponding plates of *Allocatillocrinus scoticus*, at least in several instances, and they bear fewer facets; hence they have been classed as belonging to *Allagecrinus*.

Inspection of a large amount of washings from the Morrow strata that have yielded the specimens of *Allocatillocrinus rotundus* has resulted in finding several calices of minute hypocrinids, but only three specimens smaller than 2 mm. in diameter that may be extremely juvenile representatives of *Allocatillocrinus*. They range from 1.2 to 1.5 mm. in height, which is their longest dimension. One that is illustrated (fig. 6*a*, *b*) shows the angular pentalobate form and the circlet of oral plates, and this specimen has distinct small facets on the lpR and laR only. Considered independently, the small calices are identifiable as incompletely developed examples of a *Callimorphocrinus*. They are not believed to represent a species of this genus, however, partly because so few specimens have been seen (occurrence of species of *Callimorphocrinus* commonly being represented by abundant individuals), and partly because the nodes along the angles of the cup correspond to similarly placed nodes of the lobate *Allagecrinus*-like cups that are definitely identified as youngest growth stages of *Allocatillocrinus rotundus*. These microcrinoids of *Callimorphocrinus* type are therefore regarded tentatively as belonging to *A. rotundus*. Supporting this interpretation is a study of growth stages of *Allagecrinus pecki*, n. sp., as described subsequently in this paper, for in this species the youngest forms are *Callimorphocrinus*-like individuals that carry only one or two arm facets. The rpR and laR are first differentiated as facet-bearing radials, as in the case of the specimen shown in Fig. 6*a*, *b*, but there is no clear indication of attachment for an anal series until later.

Evidence from geologic distribution

In studies of genetic relationships among fossils it is not safe to rest on the record of geologic distribution of genera, inevitably incomplete and always subject to correction coming from new finds and revised morphologic concepts. On the other hand, evidences from stratigraphic and geographic occurrence of fossil forms cannot be ignored without danger of reaching wholly erroneous conclusions.

Referring to the asymmetrical crinoids of this study, Wanner (1916, p. 7; 1924, pp. 53, 307; 1929, p. 13; 1937, pp. 108–109) concludes that general evolutionary trends are in the direction of increased simplicity of structure. In the Permian rocks of Timor, catillocrinids have fewer arm facets than forms from the Lower Carboniferous, and some of the Permian genera lack signs of the presence of an anal plate or series; allagecrinids from Timor show a preponderance that bear only five arms. Granting that the tendency to reduce parts and to simplify structural organization is evident in many crinoid stocks, it is necessary to recognize equally that parts may be increased and that structures may become cumulatively complex and specialized. If this were not true, simplification would have no place for a start.

The oldest known examples of *Allagecrinus* occur in upper horizons of the Lower Carboniferous strata of northwestern Europe. Related, more diminutive and simple crinoids, called *Hybochilocrinus* are abundant in deposits that belong to the Upper Devonian or lowermost Mississippian in Missouri. No older allagecrinids are recorded. Whatever judgment is made of some Permian crinoids that have been called *Allagecrinus*, question cannot be raised as to the generic assignment of *Allagecrinus dux* Wanner, from the Permian of Timor. This species is surprisingly similar to *A. austinii* in almost every particular.

Catillocrinus may well be regarded as marking the peak of peculiarization among multifaceted asymmetrical crinoids. It is unnecessary to repeat statements in support of this conclusion, but it is important to notice that the genus, as now defined, is restricted to lower Mississippian rocks of the central United States. Indeed, it is confined to rocks of Osage age. No ante-

cedents are known in North America and the only comparable older described crinoid is *Mycocrinus*, from Middle Devonian rocks of Germany. Although some structural features of *Allagecrinus* and *Catillocrinus* suggest relationships, there can hardly be any direct connection between them. If *Allagecrinus* descended from a *Catillocrinus*-like form, this would mean great reduction in number of arms, loss of highly specialized anal structures, considerable diminution in size, and other changes. Such an hypothesis is unreasonable. It is in conflict with ontogenetic evidence indicating development of *Allagecrinus* from a *Hybochilocrinus*-like form.

The genus *Eucatillocrinus* follows immediately the last of the recorded species of *Catillocrinus*. The former is represented in the upper crinoid zone of the Keokuk limestone at Crawfordsville, Ind., and the latter in the lower one. Structural modifications of *Catillocrinus* to form *Eucatillocrinus* are not large, and accordingly no reason is seen for doubting evolutionary change from the older to produce the younger.

Allocatillocrinus is known only from late Lower Carboniferous and early Upper Carboniferous strata, which also contain *Allagecrinus*. The lower Chester rocks of the United States that contain *Allocatillocrinus carpenteri* are not greatly different in age from beds of the Lower Limestone series of Scotland, that contain *Allocatillocrinus scoticus* and species of *Allagecrinus*. *Allagecrinus* has not been reported on this side of the Atlantic from upper Mississippian beds. *Allocatillocrinus* could have been produced out of *Allagecrinus* by addition of arms on some of the radials, and proof of this line of descent is given by ontogenetic observations already cited. This implies, however, that *Allagecrinus* antedates *Allocatillocrinus* to an unknown extent and leads to the expectation that older representatives of *Allagecrinus* will be found. *Hybochilocrinus* is only slightly removed from *Allagecrinus* and some authors class them as synonymous. In any case, this seems to carry the ancestral line of *Allocatillocrinus* to the base of the Carboniferous or into the Upper Devonian, depending on the age assignment given to the Louisiana limestone, which contains abundant examples of *Hybochilocrinus*.

Paracatillocrinus, Neocatillocrinus, Xenocatillocrinus, and *Isocatillocrinus* all occur in Permian rocks of Timor and are as yet recorded nowhere else. A gap in the record that comprises most of the Upper Carboniferous and probably some of the Permian, separates these forms from most closely related predecessors. Lines of descent must be inferred from comparative morphology. Naturally, none of these genera can have given rise to others that belong stratigraphically far below them.

Although *Callimorphocrinus* and *Trophocrinus* do not call for notice in considering the relations of *Allagecrinus* to the catillocrinids, it is desirable to add them here. *Callimorphocrinus* occurs abundantly in the Chouteau limestone (upper Kinderhook) of Missouri, as shown by samples collected by R. E. Peck, but these are undescribed. The oldest described species are found in Fern Glen (lower Osage) beds of Missouri, and the youngest occur in Permian rocks of Timor and Russia. Thus, geologic distribution harmonizes with the conclusion that *Callimorphocrinus* was derived from *Hybochilocrinus* or a closely related form by disappearance of the anal plate. *Trophocrinus* occurs in the Welden limestone (upper Kinderhook) of Oklahoma, and is seemingly an offshoot from the stock that produced *Callimorphocrinus.*

LINES OF EVOLUTIONARY DEVELOPMENT

Origin of allagecrinids and catillocrinids

Studies of the source or sources of the Late Paleozoic asymmetrical crinoids having numerous unbranched arms encounter many problems. Inquiry as to varied lines of evolutionary development likewise meets many problems. These difficulties are inherent in the great incompleteness of the paleontologic record and in the deficiencies of knowledge concerning crinoid structures. The catillocrinids are not abundant. Some genera are recognized on the basis of a single specimen and some species are represented by only two or three specimens. Allagecrinids are more common but they are inconspicuous. Search for them is bound to yield much new information. The nature and significance of morphologic characters of these crinoids are only partly

understood, questions being very much open on such matters as the "infrabasals" of the genotype of *Catillocrinus*, the almost unlimited addition of arms and facets on some radial plates, and development of various anal elements. Discussion of evolutionary development is guided by several reliable sign-posts but trails between some of these and leading up to the first ones are easily lost.

Origin of the crinoid stocks under consideration is confidently placed within the circle of Silurian forms that includes the Pisocrinidae and Synbathocrinidae. The latter are relatively simple, nearly symmetrical, moderately stable crinoids that seem to have branched at an early point in development from heterocrinid ancestors. The synbathocrinids have some characters in common with pisocrinids, catillocrinids, and allagecrinids. They might contain the source of the line leading to *Callimorphocrinus*, *Allagecrinus*, *Allocatillocrinus*, and others but not that to *Catillocrinus*. The Synbathocrinidae persisted into the Permian, living as neighbors of the variously specialized forms that are derivatives from their own or a closely related line. The Pisocrinidae retain heterocrinid structural irregularities of the radial circlet and otherwise possess structural characters that should be found in the ancestral stock of catillocrinids and allagecrinids. It is logical to conclude that this family gave rise to the younger groups just mentioned (see Bather, 1893, p. 25; 1900, p. 150; Jaekel, 1895, p. 44; Springer, 1923, p. 4; Wanner, 1929, p. 12), as well as to the Haplocrinidae. The Calceocrinidae, which show marked asymmetry and characters of arm arrangement that are suggestive of *Catillocrinus* (see Wachsmuth and Springer, 1886, pp. 267–281), were probably developed independently from Ordivician heterocrinids, as indicated chiefly by features of arm branching.

Pisocrinus has two large radials (aR, lpR) and three small ones (fig. 7) just as is the case in *Mycocrinus*, *Catillocrinus*, *Eucatillocrinus*, and *Paracatillocrinus*. Furthermore, in all the named genera it is precisely the same plates that are greatly enlarged. *Pisocrinus* has only five arms, but the form and structure of these are entirely similar to those of the catillocrinids. It is plausible

to conclude that *Catillocrinus* and the allied genera mentioned are derivatives of a crinoid stock having the structural plan that is expressed in *Pisocrinus*.

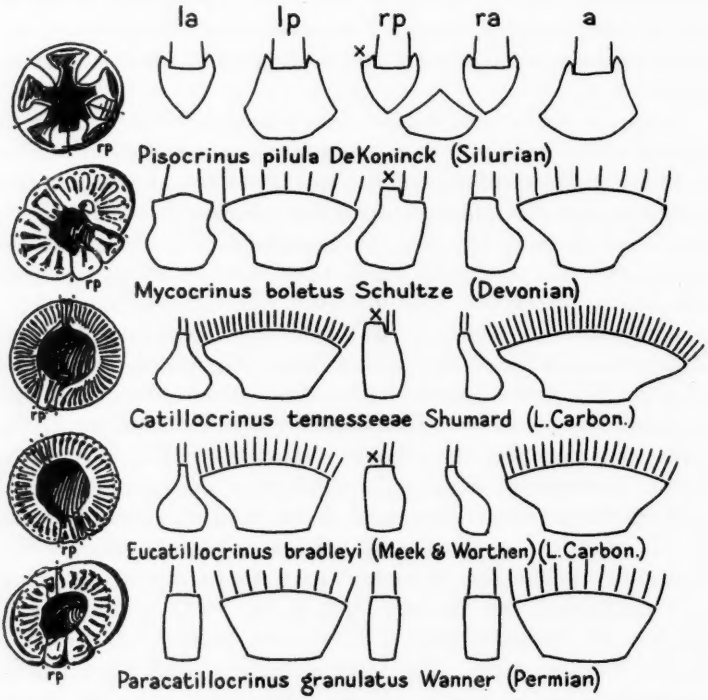

FIG. 7.—Diagrams the arm facets and the asymmetry in distribution of arms and form of radials in the genotype species of *Pisocrinus*, *Mycocrinus*, *Catillocrinus*, *Eucatillocrinus* and *Paracatillocrinus*. All of these genera are distinguished by enlargement of the anterior and left posterior radials, and they bear other resemblances that indicate close relationship.

Allagecrinus, *Allocatillocrinus*, and *Neocatillocrinus*, as well as *Xenocatillocrinus* and *Isocatillocrinus*, differ from the group just considered in the enlargement of the raR and presence of multiple facets on this plate, in addition to the aR and lpR. This is a distinction that seems to indicate a line genetically different from

that in which the raR persists as a slender one-armed plate. The *Allagecrinus-Allocatillocrinus* line may also arise from a *Pisocrinus*-like ancestral form. Fusion of the raR and the inferradial below this plate in *Pisocrinus*, instead of disappearance of this inferradial, would produce three large radials and two small ones, as in the typical plan of *Allagecrinus* and *Allocatillocrinus*. The nature of developments along this line may be inferred from study of *Calycanthocrinus* Schultze, an asymmetrical crinoid having more than five unbranched arms, from the Middle Devonian of Germany (see fig. 8). In this genus each of the slender uniserial arms is supported by a separate radial plate, some of which are designated as pararadials, or accessory radials. Three of the radials (lpR, aR, raR) are definitely larger than others and it is these same plates that are largest in *Allagecrinus*, *Allocatillocrinus*, and *Neocatillocrinus*. Bather (1900, p. 150) points out that the pararadials of *Calycanthocrinus* are morphologically the same as primibrachs and that fusion of these plates with the adjacent subtending radial would develop multifaceted radials bearing several simple arms. No crinoids other than *Allagecrinus* and the catillocrinids exhibit this peculiar structure. Thus, *Calycanthocrinus* seems to be a connecting link between typical pisocrinids and succeeding multifaceted crinoids. In *Calycanthocrinus decadactylus*, the genotype species, five arms are borne by the part of the radial circlet belonging to the anterior and right anterior rays. Combining the radial elements, as shown in figure 8, the structural plan corresponds strikingly to that of *Allagecrinus austinii* even including the direction of overlap of radials near the summit. Accordingly, *Allagecrinus* and allied forms are thought to have originated from a representative of the Pisocrinidae. It is also believed that the *Allagecrinus* line of development is distinct from the one leading to *Catillocrinus*.

Evolution of radial asymmetry

Radial asymmetry is correlated with the number of arms borne by particular plates of the circlet. No one is likely to dissent from the conclusion that a cup in which 90 percent of the periphery of the summit is occupied by arms belonging to two RR,—

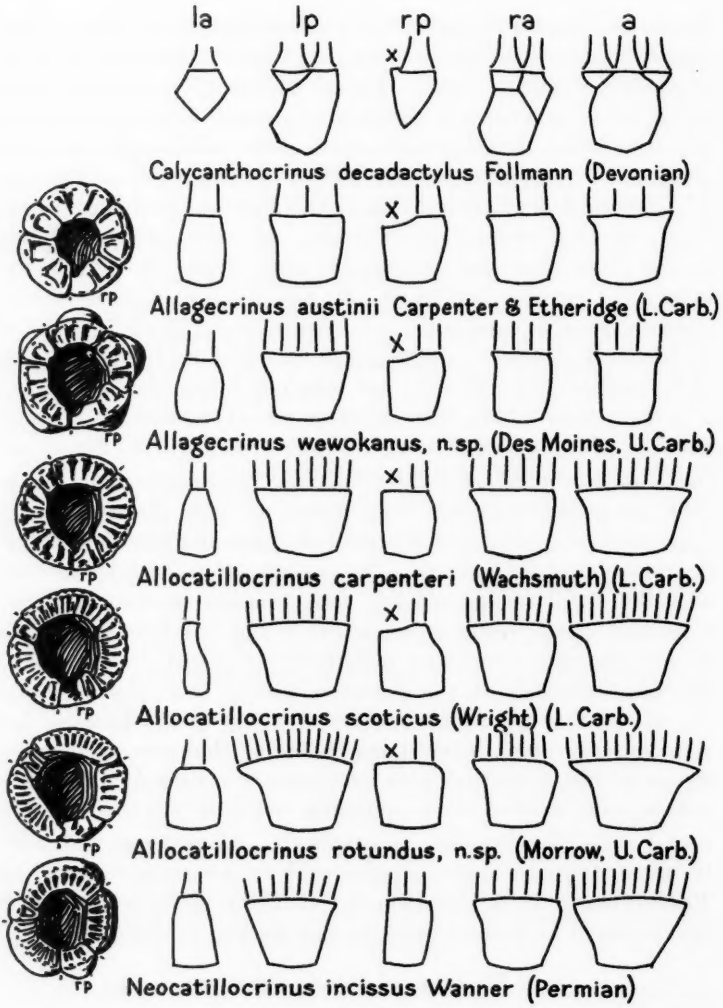

FIG. 8.—Diagrams showing the arm facets and asymmetry in the distribution of arms and form of radial plates in representative species of *Calycanthocrinus*, *Allagecrinus*, *Allocatillocrinus* and *Neocatillocrinus*. The drawings are arranged to show the interesting, apparently significant correspondence in general plan, which includes similarity in the direction of encroachment in summit portions of certain radials on their neighbors.

the remaining 10 percent representing 3 RR,—is a much more specialized crinoid than one in which the RR are subequal. Great enlargement of some plates at expense of others obviously represents a departure from the normal plan of crinoid cups. The peak of such specialization was attained in *Catillocrinus*, but the steps leading up to this form are unknown. *Mycocrinus*, although older and having fewer facets, seems to stand outside of the direct line of ancestry because of its very thick fused base and other peculiarities. Descendants of *Catillocrinus* or of the stock from which this genus was directly evolved are thought to include *Eucatillocrinus* and probably *Paracatillocrinus*. These genera show like asymmetry of the radial circlet, having two very large radials and three small ones. The fact that they possess fewer arms than *Catillocrinus* indicates a reversal of the trend toward multiplication of arms.

Most symmetrical among the crinoids under discussion is *Callimorphocrinus*. Next are *Hybochilocrinus* and *Allagecrinus*. If *Callimorphocrinus* grew out of *Hybochilocrinus*, as inferred by Weller (1930, p. 13), and Peck (1936, p. 283), the trend of this evolutionary change was toward symmetry and away from asymmetry. There was no development beyond *Callimorphocrinus* in its line. *Allagecrinus*, which likewise ssems logically to have been derived from a *Hybochilocrinus*-like ancestor, shows progressive increase of radial asymmetry and a tendency to increase the number of arm facets on radials except the rpR and laR. Continuation of these trends leads into *Allocatillocrinus*. The appearance in Permian catillocrinids of multiple facets on the rpR and finally on the laR, reverses the tendency toward increased radial asymmetry.

Distribution of the inequality in size of the RR and the number of arms borne by them seems to be more variable in *Allagecrinus* than in genera that have been referred to the Catillocrinidae. This suggests that *Allagecrinus* comprises a plastic stock that is capable of differentiation in various directions. All species show much variation in characters of the lpR, aR, and raR.

The origin of characters seen in *Neocatillocrinus*, *Xenocatillocrinus*, and *Isocatillocrinus* offer somewhat special problems. The first two are similar to *Allagecrinus* and *Allocatillocrinus* in

having only a single arm on the relatively narrow laR plate. They differ in having two or more arms on the rpR. Each of the RR of *Isocatillocrinus* has several arms. If addition of arms on the aR, raR, and lpR is an established sort of evolutionary change, one may ask whether similar modification might not extend at some point to affect the normally stable one-armed rpR and, ultimately, the laR. The nature of the changes is the same, and therefore no reason is found to exclude possibility that these Permian genera were derived from such a form as *Allocatillocrinus*. The only opposing evidence is the record of long persistence of the one-arm-bearing radials so as to establish this as one of the most stable of generic characters.

Development of multiple-armed radials

The tendency toward increased number of the arms attached to some radials, which is a distinguishing feature of allagecrinids and catillocrinids, seems to be an example of orthogenesis. Widening of radial summits and accompanying increase of arms may be accounted for by fusion of the primitive radial element with successively proliferated axillaries. This was suggested in making comparisons with *Calycanthocrinus* and it may be illustrated further by reference to *Calceocrinus* (see fig. 9). The latter genus, of Silurian and Devonian age, is a crinoid of greatly disturbed symmetry whose ancestry is traced by Bather (1900, p. 148) to an Ordovician form having heterocrinid structure. *Calceocrinus* is not closely related to any of the genera discussed in this paper but the arrangement of its arms is decidedly interesting as regards the problem of the multifaceted catillocrinid and allagecrinid radials. The laR commonly bears only one arm, but the adjoining radials carry several arms, the lower axillaries being so placed that it is easy to see how fusion of them would produce just the sort of structure we are seeking to understand. Seemingly it was development of such a nature that was found to be useful in the catillocrinid stock. Once well started, it went on. Addition of a new facet and arm was no more of a trick than the bifurcation of the terminal part of a branch and it has essentially no more morphological significance. As long as

an individual of a species continued to grow, seemingly it continued to add to its equipment of arms, at least in some genera and species. The rate of increase of facets on individual radials is a specific character that is approximately constant, but there

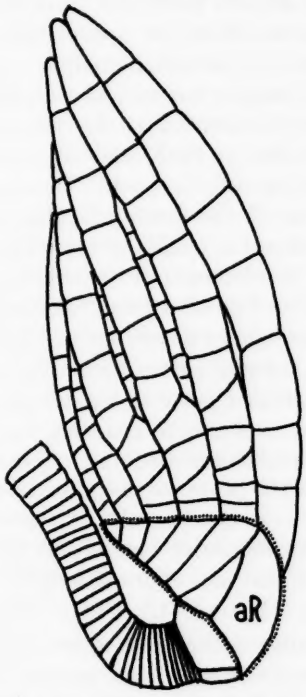

FIG. 9.—Anterior view of the crown of a specimen of *Calceocrinus* showing the arm structure of one of the rays. The anterior radial and lower brachials attached to it are outlined by a heavy line in order to indicate how fusion of these plates would produce a multifaceted radial plate bearing several parallel arms, as in catillocrinids. *Calceocrinus* is an asymmetrical crinoid occurring in Silurian and Devonian rocks. (Modified from Bather.)

are variations. Evidence is conclusive that some radials never bear more than a single arm, although this one may be notably larger than the many slender arms of an adjoining large radial plate. These characters are of generic importance.

Order of development of arms.—A deduction that may be added concerns the position of the newly added arms on multifaceted radials. If the mode of development of the arms is correctly explained, as given in the last paragraph, it follows that new arms should appear in a definite place and in definite order on each radial. Youngest arms should be grown only at one or both of the lateral extremities of the radial summit. In case addition of arms proceeded at a single extremity of the radial, obviously the oldest arm of the ray is located at the opposite extremity. In case addition proceeded at both ends of a radial summit, the oldest arm must be centrally located. These conclusions can be tested. Examination of the facets of allagecrinids and catillocrinids frequently shows a readily perceptible difference in the size or sharpness of development of certain facets. For example, every specimen of two lots of *Allocatillocrinus*, comprising more than 20 dorsal cups, shows a well-formed facet of larger than average size at the anterior extremity of the raR and a smaller, generally less well defined facet at the posterior extremity. In some instances there is doubt in counting the number of facets on this plate because of uncertainty as to whether or not a facet can be recognized at the posterior margin; there is no such doubt about the anterior end of the raR. Greatest summit length (measured normal to the outer face of the plate) of the raR is close to the anterior end and shortest length is at the posterior end (see figs. 6k, m, o, q and 14i). These observations indicate that newly added arms on this plate appear only at the posterior extremity, which is the margin that encroaches laterally on its neighbor, the rpR.

The anterior radial (aR) encroaches on both adjoining plates, has greatest summit length in the middle part, and least well formed facets at the two extremities; presumably the first-formed arm is centrally located on this plate (see figs. 6, 14). The left posterior radial (lpR) is less certainly interpreted. New arms are added at the anterior extremity where this plate crowds against the laR, and they may be added also at the posterior margin, although this border does not bear evidence of growth at the expense of the rpR; greatest length of the summit is somewhat

centrally located but nearer to the posterior than the anterior extremity (fig. 14c). These considerations apply also to *Allagecrinus* but observations are less definitely made.

CLASSIFICATION

The foregoing discussion of crinoids that until now have been classed as belonging to the two families called Allagecrinidae and Catillocrinidae indicates ground for revision of classification. It is natural under circumstances of former less complete knowledge that these crinoids should have been referred to different families. Placement of these families in different suborders, however, denotes either a very large misunderstanding of true relationships of these groups or faulty definition of the suborders, or both. It is phylogenetically inconceivable that a genus actually belonging to the family Catillocrinidae in the suborder Fistulata can be direct development out of a genus properly classified as belonging to the family Allagecrinidae in the suborder Larviformia, unless it is granted that this connecting link marks the point of origin of the Fistulata. Nevertheless, evidence presented indicates that *Allocatillocrinus* is thus derived from *Allagecrinus*. Difficulties are not resolved in this case by revision of generic concepts nor are they disposed of satisfactorily simply by transfer of a genus or genera from one family to the other. There is need for a complete realignment in the light of all the known relationships.

The present study has indicated that one group of these crinoids, including *Mycocrinus*, *Catillocrinus*, *Eucatillocrinus*, and *Paracatillocrinus*, is characterized by the development of many arms on but two of the radials, the lpR and aR. This group seems not to contain in any known form the direct ancestor of the other main group, which comprises the allagecrinids and so-called catillocrinids except those just named. Advanced types of the second group are characterized by development of three or more multifaceted radials. Origin of these from an independent branch of the ancestral pisocrinid stock is indicated by persistent differences in structure, even though some of them are parallel with features of the other, and by ontogenetic evidence. The distinction between the two groups is one that in

my judgment cannot be rated important enough to warrant recognition of two families. Collectively they seem to be classified best as a single family that contains two subfamilies. Proposal is made to revise classification in this manner.

Now presented is the question whether the family containing the whole assemblage should be designated as the Allagecrinidae or the Catillocrinidae. The family Allagecrinidae was proposed by Carpenter and Etheridge in 1881, and the family Catillocrinidae was proposed by Wachsmuth and Springer in 1886. The Zoological Rules do not make specific provision for nomenclature of families on the basis of priority, but good practice supports this procedure. As when two genera are combined, the name of the older prevails, so in the case of families, it seems necessary here to suppress the designation Catillocrinidae and to employ the family name Allagecrinidae. The subfamilies are designated Catillocrininae and Allagecrininae respectively. An outline of the revised classification follows.

Outline of Revised Classification

Family ALLAGECRINIDAE Carpenter and Etheridge (1881), emend. Moore.—Small, monocyclic crinoids, mostly asymmetrical, having distally thickened radials that each bear facets for attachment of one to many arms; facets generally marked by a transverse ridge, by a dorsal canal opening, and on the inner side by a groove that is bounded by longitudinal ridges. Arms, slender, unbranched, nonpinnulate, ranging in number from 5 to an observed maximum of 58. Dorsal cup low, truncate bowl- or cone-shaped to stelliform, the base mostly covered by large proximal stem segments. Orals present in immature stages and in very diminutive adult forms. Anal plate and series strongly developed in some genera but absent in others. Stem round to somewhat elliptical, typically tapering distally. *Occurrence.*—Devonian to Permian; Europe, North America, East Indies.

Subfamily CATILLOCRININAE, n. subf.—Dorsal cup strongly asymmetrical, marked by great enlargement of two radials (rpR and aR), which bear numerous arms. *Occurrence.*—Devonian to Permian; Europe, North America, East Indies.

Genus MYCOCRINUS Schultze (1865).—BB circlet thick, massive, forming at least half of total height of cup, consisting of 2 or 3 more or less fused plates. The rpR carries an elevated process on the left shoulder for support of an anal plate. Arms 11 to 17. *Genotype.—M. boletus* Schultze. *Occurrence.*—Middle Devonian; Germany.

enus CATILLOCRINUS Shumard (1866), (*Nematocrinus*

Meek and Worthen, 1866).—BB 3 to 5, mostly covered by stem, in some species associated with a centrally located low cone of paper-thin plates that have been interpreted as IBB and also as an internal structure, not part of the dorsal cup. RR very asymmetrical, consisting of very large lpR and aR that bear very numerous arms, the other RR small and each bearing only a single arm. A raised process on the left shoulder of the rpR supports a large anal plate that interlocks with a massive anal tube extending to or beyond the ends of the arms. Stem round with proximal enlargement. *Genotype.—C. tennesseeae* Shumard. *Occurrence.*—Lower Mississippian, Osage stage; Kentucky, Tennessee, Iowa, Indiana.

Genus EUCATILLOCRINUS Springer (1923).—Cup relatively high, truncate cone-shaped. BB 3, sutures obscure, circlet mostly covered by stem. Summit of rpR even, the left part articulating with the first tube plate of the anal sac which is very long. Arms 40 to 46. *Genotype.—Catillocrinus bradleyi* Meek and Worthen. *Occurrence.*—Keokuk limestone, Osage stage, lower Mississippian; Indiana.

Genus PARACATILLOCRINUS Wanner (1916).—Cup low, discoid, somewhat obliquely set on stem. BB 3, more commonly 2, or fused to a single plate, mostly covered by the proximal stem segment. Sutures between RR straight; rpR without articulation for an anal tube plate and anal sac shrunken or lacking. Stem elliptical, expanding towards cup. Arms 13 to 24. *Genotype.—Paracatillocrinus granulosus* Wanner. *Occurrence.*—Permian; Timor.

Subfamily ALLAGECRININAE, n. subf.—Dorsal cup truncate bowl- or cone-shaped to stelliform symmetrical in some microscopic forms but mostly having strong asymmetry. BB 3 or fused together. RR 5, equal to very unequal, 3 plates of this circlet (lpR, aR, raR) typically larger than the others and multiple-armed, but included forms range from cups having a single facet on each radial to those having all RR multifaceted. Anal series present or absent. Stem round, expanding toward cup, the proximal segment covering most of the BB. *Occurrence.*—?Upper Devonian to Permian; Europe, North America, East Indies.

Genus HYBOCHILOCRINUS J. M. Weller (1930).—Calyx subpyriform, very small, height 1.5 mm. or less. Orals persist in adults. Distinguished by presence in mature stages of an anal plate that rests on the beveled left shoulder of the rpR. *Genotype.—Allagecrinus americanus* Rowley. *Occurrence.*—Louisiana limestone, Upper Devonian or lowermost Mississippian, and Chouteau limestone, lower Mississippian (Kinderhook); Missouri.

Genus CALLIMORPHOCRINUS J. M. Weller (1930).—Calyx subpyriform, lobate to stelliform, very small, height gen-

erally 2 mm. or less. Orals persist in adults. RR equal. Anal plate absent. *Genotype.—Callimorphocrinus astrus* J. M. Weller. *Occurrence.*—Lower Mississippian (Chouteau limestone) to Permian; North America, Europe, East Indies.

Genus TROPHOCRINUS Kirk (1930).—Calyx subpyriform, modified by protuberance of upper part of left RR as a pouch that may rise higher than the orals, very small, height less than 1.5 mm. Anal plate absent. *Genotype.—Trophocrinus tumidus* Kirk. *Occurrence.*—Lower Mississippian (Chouteau); Oklahoma, Missouri.

Genus ALLAGECRINUS Carpenter and Etheridge (1881).—Dorsal cup truncate cone-shaped to stelliform, small, greatest dimension in adult stage ranging from about 1.5 to 6 mm. RR nearly equal to strongly unequal, the rpR and laR invariably characterized by the presence of one arm facet on each, others having a variable number of facets to a maximum of 6 on one plate; facets marked by a distinct transverse ridge and dorsal canal opening. Arms equal or unequal in size, 6 to ?16. Orals may persist to early adult stage but are generally not preserved. An anal series rests on the left shoulder of the rpR, which may be distinctly beveled. *Genotype.—Allagecrinus austinii* Carpenter and Etheridge. *Occurrence.*—Lower Carboniferous (upper part) to Permian; Europe, North America, East Indies.

Genus WRIGHTOCRINUS, n. gen.—Calyx pyriform, small height ranging from about 1.5 to 4.5 mm. Radial circlet asymmetrical, characterized by narrow laR and raR that each bear one arm, and by wide other RR that each bear two or more arms. A small anal plate appears in the notch between the posterior RR in one species (*W. biplex*) but is seemingly lacking in the genotype. Orals persist in adult stage. *Genotype.—Allagecrinus jakovlevi* Wanner. *Occurrence.*—Lower Carboniferous (upper part), Scotland, and Permian, Timor.

Genus ALLOCATILLOCRINUS Wanner (1937).—Dorsal cup truncate cone- to bowl-shaped, width a little greater than height, small, about 3 to 12 mm. in greatest width. Radial circlet strongly asymmetrical, being characterized by two small plates (rpR and laR) that each bear a single arm, and three large plates that each carry several arms. The total number of arms ranges from about 13 to 42. An anal series is attached to the left shoulder of the rpR, which is beveled or even with the summit of the radial. *Genotype.—Allagecrinus carpenteri* Wachsmuth. *Occurrence.*—Lower Carboniferous (upper part), Illinois, Indiana, Alabama, Scotland; Upper Carboniferous (lower part), Oklahoma.

Genus NEOCATILLOCRINUS Wanner (1937).—Dorsal cup low bowl-shaped, width about 9.5 mm., obliquely placed on stem.

Anal series lacking. Similar to *Allocatillocrinus* except in having two arm facets on the rpR instead of one facet and attachment for an anal series. *Genotype.*—*Neocatillocrinus incissus* Wanner. *Occurrence.*—Permian, Timor.

Genus XENOCATILLOCRINUS Wanner (1937).—Dorsal cup

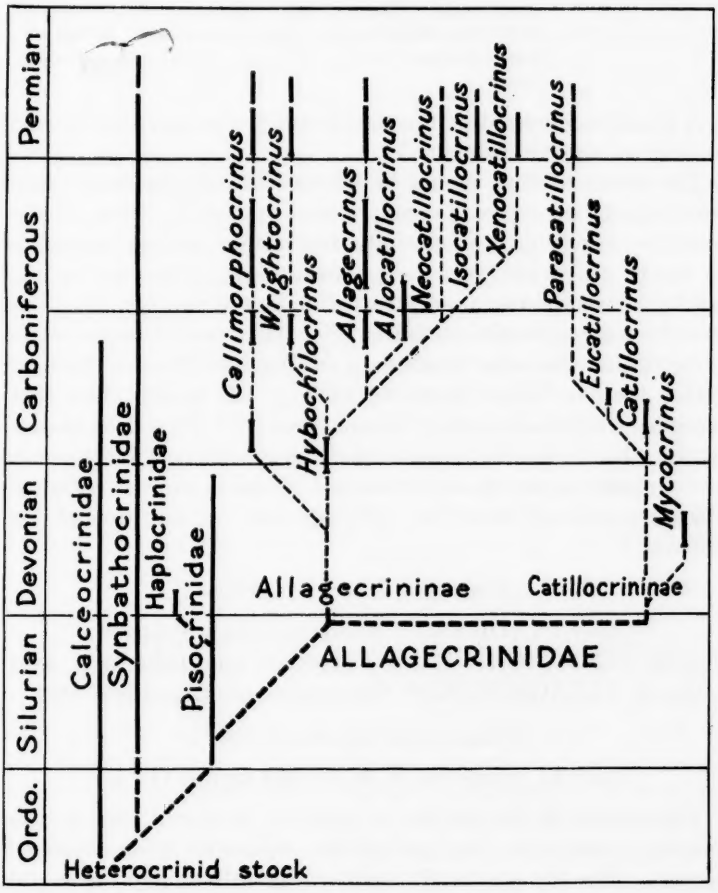

FIG. 10.—Diagram showing the geologic distribution and inferred phylogenetic relations of the family Allagecrinidae Carpenter and Etheridge (emend.).

low, uneven, greatest width about 10.5 mm. RR notably dissimilar, all multifaceted except the laR, which bears a single unusually large arm. An anal series is present on the left shoulder of the rpR. *Genotype.*—*Xenocatillocrinus wrighti* Wanner. *Occurrence.*—Permian, Timor.

Genus ISOCATILLOCRINUS Wanner (1937).—Dorsal cup low, greatest width about 14.5 mm. RR nearly equal in size and all of them multifaceted. Anal series absent. *Genotype.*—*Isocatillocrinus indicus* Wanner. *Occurrence.*—Permian, Timor.

A diagram representing the classificatory relations and inferred phylogeny is given in Figure 10.

The problems that cannot be avoided in defining major divisions among the crinoids ramify almost endlessly. Some of the questions touch the present study, but it does not seem desirable to try to deal with them here. Accordingly, placement of the family Allagecrinidae, as constituted under the new concepts that have been given, is left indefinite. For the present it seems better to recognize the order Inadunata of Wachsmuth and Springer rather than to follow Bather's (1900, p. 94) classification that recognizes subclasses called Monocyclica and Dicyclica, respectively. It is believed, however, that the suborders of Wachsmuth and Springer named Larviformia and Fistulata are not recognizable or usable divisions in a phylogenetic classification of the crinoids.

DESCRIPTION OF NEW SPECIES

Order INADUNATA Wachsmuth and Springer

Family ALLAGECRINIDAE Carpenter and Etheridge, 1881

Genus ALLAGECRINUS Carpenter and Etheridge, 1881

Allagecrinus dignatus, n. sp.

Plate II, figures 5a, b, 6a, b; text figures 11 i–l.

Description of this species is based on 15 dorsal cups of distinctive appearance that are readily separated from described species. The cup is strongly stelliform in outline, and the height is little greater than half of the greatest width.

The basal circlet is very low, consisting of three obscurely defined plates, the small B being definitely identified in some

specimens, however, and located in the posterior interradius. The BB are almost entirely covered by the proximal stem segment, beyond which the distal parts slope steeply upward.

The RR are distinctly unequal in size and rather strikingly bulbous in form. The proximal parts, typically, are tangent to the basal plane of the cup. In a few specimens the downward bulge of the RR is so pronounced that the bottom of the BB circlet is lifted about 0.3 mm. above the basal plane of the cup. The median and distal mid-portion of the RR is produced in a sharply rounded bulge, which may have a keel-like form, and on each side of this is a much fainter bulge that does not include a narrow lateral border of the plates. Thus, along each of the interradial sutures is a narrow, somewhat flat-bottomed pathway that seems sharply set apart from the adjacent bulging parts of the RR. Each of the RR has a more or less distinct trilobate form. The lpR is separated at a glance from the other RR because of its marked asymmetry of form, and the unusual prominence of the bulge at the left of the mid-line. The adjoining laR is distinctly smaller than any other plates of the radial circlet.

Very little variation is observed in the size of the specimens, but three that are a little smaller than the others seem to be immature forms. Eleven of the 12 specimens regarded as adults have an identical arrangement of facets on the summit of the RR, as follows: lpR, 3; laR, 1; aR, 2; raR, 2; rpR, 1. One specimen (paratype no. 458911H) differs from the others in having 3 facets on the aR, instead of 2, and this cup has greatest observed width, amounting to 5.4 mm. Three specimens (paratypes 458911K, L, M), which are a little smaller than average (greatest width about 4 mm), differ from the average in having only 1 facet on the aR instead of 2. The posterior interradius is easily recognized by the smaller width of the left distal portion of the rpR, which produces a marked indentation in the outline of the body cavity, but the left shoulder of this plate is so slightly depressed that a notch is hardly perceptible. The large size and irregular form of the lpR makes it readily recognizable. The summit of the laR is distinctly below the summit levels of adjoining plates. Lateral encroachment of the distal portions of the RR, following

the plan of catillocrinids as already described, is readily seen on most specimens. The surface of the cup is entirely smooth.

The greatest width of the holotype specimen is 4.8 mm, height of cup 2.4 mm; width of BB circlet 2.0 mm; width of proximal margin of each R 1.3 mm.

Remarks.—This species seems to be most closely similar to *A. strimplei* Kirk (figs. 2b, 11a–d) from the Dewey (Drum) limestone, but cups of the latter species are less strongly stelliform, the RR are more evenly rounded and higher above the basal plane of the cup, the surface is ornamented by fine granulations, and, probably most significant, the distribution of arm facets is somewhat constantly different. Of 15 specimens of *A. strimplei* available for present study by me, the arm facets are clearly visible on 10, and without exception these show the following distribution: lpR, 2; laR, 1; aR, 1; raR, 2; rpR, 1. Accordingly, it seems that *A. strimplei* has normally one less arm facet on the lpR and one less on the aR than in *A. dignatus*.

Occurrence.—Upper part (Altamont) of Oologah limestone, Marmaton group, Des Moines stage, Pennsylvanian (Upper Carboniferous); Kansas University loc. 4589, Garnett quarry, about 7 miles north of Tulsa, Oklahoma; collected by Bob Stevens.

FIG. 11.—Camera lucida drawings of dorsal cups of species of *Allagecrinus*.

a–d, Allagecrinus strimplei Kirk, dorsal, posterior, ventral, and anterior views of a dorsal cup of a topotype specimen (Univ. Kansas no. 60782) from the Dewey (Drum) limestone, at Dewey, Okla.

e–h, Allagecrinus bassleri Strimple, dorsal, posterior, ventral and anterior views of a dorsal cup of a typical example (Univ. Kansas no. 45514) a topotype from the upper Ochelata (Stanton horizon) at the Mound, Bartlesville, Okla.

i–l, Allagecrinus dignatus, n. sp., dorsal, posterior, ventral and anterior view of the holotype specimen (Univ. Kansas no. 458911A), from the Oologah limestone at Garnett quarry, 7 miles northeast of Tulsa, Okla.

m,n, Allagecrinus constellatus, n. sp., dorsal and ventral views of the holotype specimen (Univ. Kansas. no. 458912A), from the Oologah limestone at Garnett quarry, 7 miles northeast of Tulsa, Okla.

o, Allagecrinus garpelensis Wright, ventral view of a young specimen showing the oral plates in position and basal part of the anal series (in center, below); primibrachs are attached to the radial facets except on the aR (after James Wright, 1932) × 7.5. Upper limestones of the Carboniferous Limestone series, Muirkirk, Scotland.

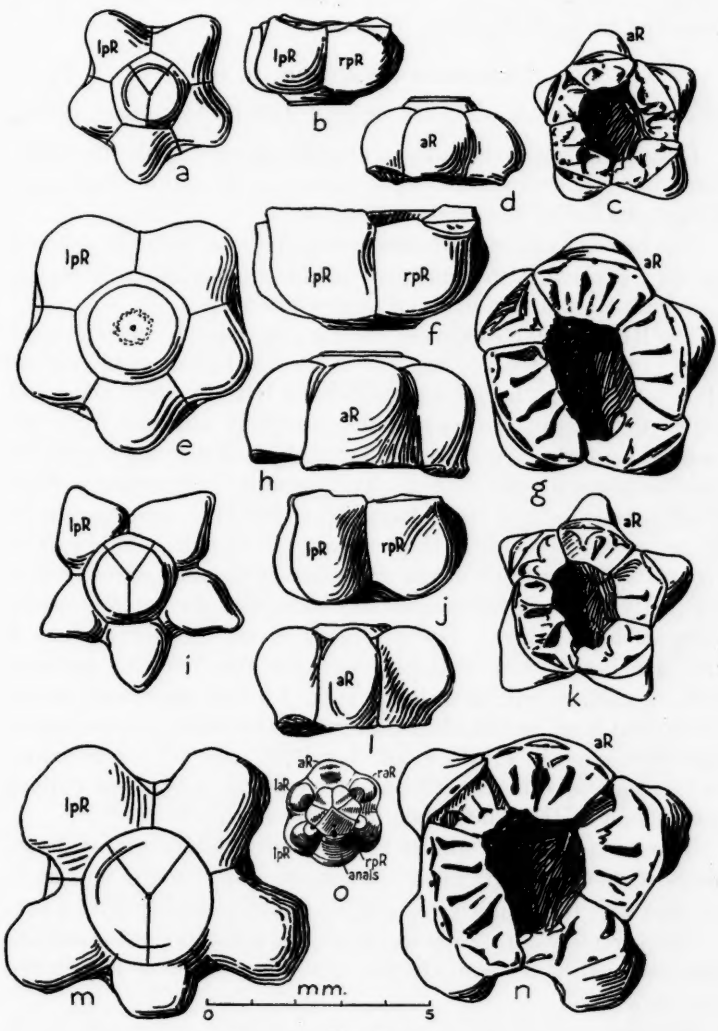

FIG. 11

Types.—Holotype, no. 458911A, paratypes, nos. 458911B–N, deposited in U. S. National Museum.

Allagecrinus constellatus, n. sp.

Plate II, figures 1–4; plate III, figure 4; text figures 11m,n, 12a–h.

Dorsal cup relatively large in mature specimens, bluntly stelliform, but RR somewhat sharply pointed in immature specimens. Height one half of the greatest width or less.

The basal circlet is extremely low and almost entirely covered by the proximal stem segment. It is composed of three plates, the small B occurring in the posterior interradius.

The RR of young specimens having a moderately steep upward slope in the mid-area are tangent to the basal plane of the cup or almost touch it. In older examples the RR are above the basal plane of the cup, projecting subhorizontally outward from the proximal suture, then rising subvertically and curving inward to the facet-bearing distal area. The posterior interradius is most readily recognized by the indentation of the body cavity produced by reduction in width of the left part of the rpR. This part of the plate for reception of the first plate of the anal series bears a distinctly visible notch in some specimens, but the notch is hardly perceptible in others. Six specimens reveal the distribution of the arm facets, and of these four have the following pattern: lpR, 3; laR, 1; aR, 2; raR, 3; rpR, 1. One specimen has an additional facet on the aR, making 3 on this plate; the remaining specimen has lpR, 4; laR, 1; aR, 3; raR, 3; rpR, 1. Irregularities in the height of different RR and in overlap at their distal margins correspond to those described in *A. dignatus*.

The surface of this species is marked by closely spaced, large, rounded to stellate granules. These are almost coarse enough to be seen with the unaided eye, and are readily observed with a lens.

Measurements of a large specimen, the holotype, are as follows: greatest width, 6.6 mm; height, 2.7 mm; width of BB circlet, 3.0 mm.

Remarks.—This species seems most closely comparable to *A. bassleri* Strimple (see figs. 2a, 11e–h), but comparison with several good examples of the latter species shows that *A. constellatus* is

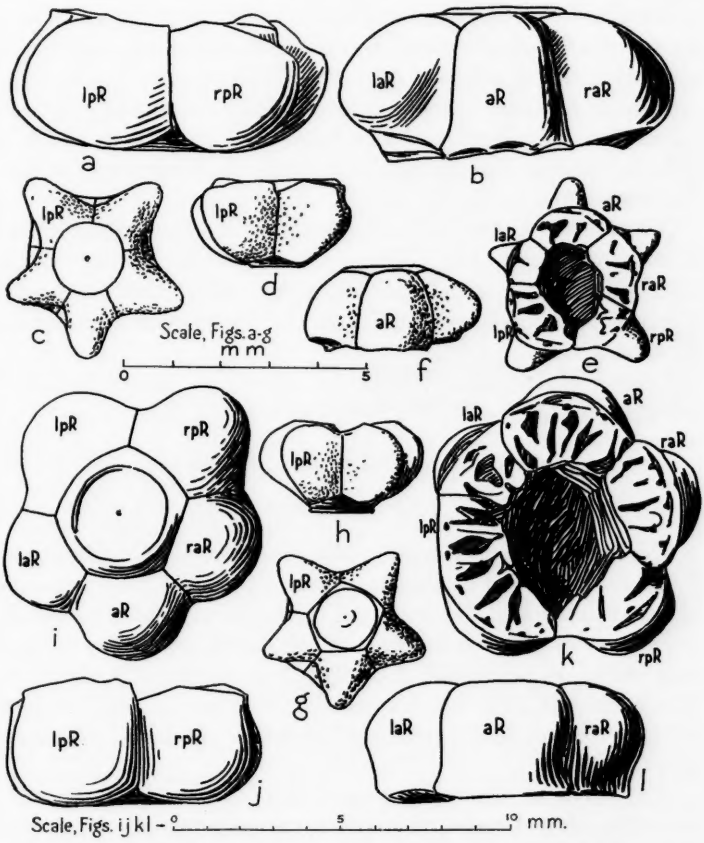

FIG. 12.—Camera lucida drawings of dorsal cups of species of *Allagecrinus*.

a–h, Allagecrinus constellatus, n. sp., from the Oologah limestone, Garnett quarry, 7 miles northeast of Tulsa, Okla. *a,b*, Posterior and anterior views of the holotype (Univ. Kansas no. 458912A). *c–f*, Dorsal, posterior, ventral and anterior views of a young paratype (Univ. Kansas no. 458912D). *g,h*, Dorsal and posterior views of a young paratype (Univ. Kansas no. 458912E).

i–l, Allagecrinus sp., cf. *A. bassleri* Strimple, dorsal, posterior, ventral and anterior views (Univ. Kansas no. 60531), from the Wewoka formation at dam about 6 miles southwest of Okmulgee, Okla.

readily separated by the more strongly protuberant nature of the RR, and the coarser nature of the surface ornamentation. Strimple reports the distribution of arms on specimens of *A. strimplei* of varying size as follows: lpR, 3 to 5; laR, 1; aR, 1 to 4; raR, 2 to 3; rpR, 1. Three topotypes of *A. bassleri* studied by me have a constant arrangement of arms showing lpR, 4; laR, 1; aR, 3; raR, 3; rpR, 1; this is the same as in the largest specimen of *A. constellatus*.

Occurrence.—Upper part (Altamont) of the Oologah limestone, Marmaton group, Des Moines stage, Pennsylvanian (Upper Carboniferous); Kansas University loc. 4589, Garnett quarry, about 7 miles northeast of Tulsa, Oklahoma; collected by Bob Stevens.

Types.—Holotype, no. 458912A; paratypes nos. 458912B–H; deposited in the U. S. National Museum.

Allagecrinus pecki, n. sp.

Text figures 13*a–n*

Specimens of a previously undescribed species of *Allagecrinus*, found by Raymond E. Peck, of the University of Missouri at two localities in central Missouri, are of special interest because they show a series of growth stages. The young specimens have the oral circlet in place but it is absent in the mature specimens. These crinoids, 13 in number, which come from the topmost layers of the Cherokee shale, are described under the name *Allagecrinus pecki*, n. sp.

The calyx of very young specimens is sharply stelliform in dorsal or ventral view and somewhat rounded in side view, greatest width slightly exceeding the height; the RR project in the form of pointed or serrate crests that extend laterally farthest at midheight of the calyx; the oral circlet is low, evenly rounded, its plates centrally hollowed, and as a whole it comprises one third of the height of the calyx and about one half of its greatest width. As growth proceeds, the RR become gradually less keeled and pointed, but the calyx retains its stellate outline into maturity. The largest observed cups have a pentalobate form, the RR being

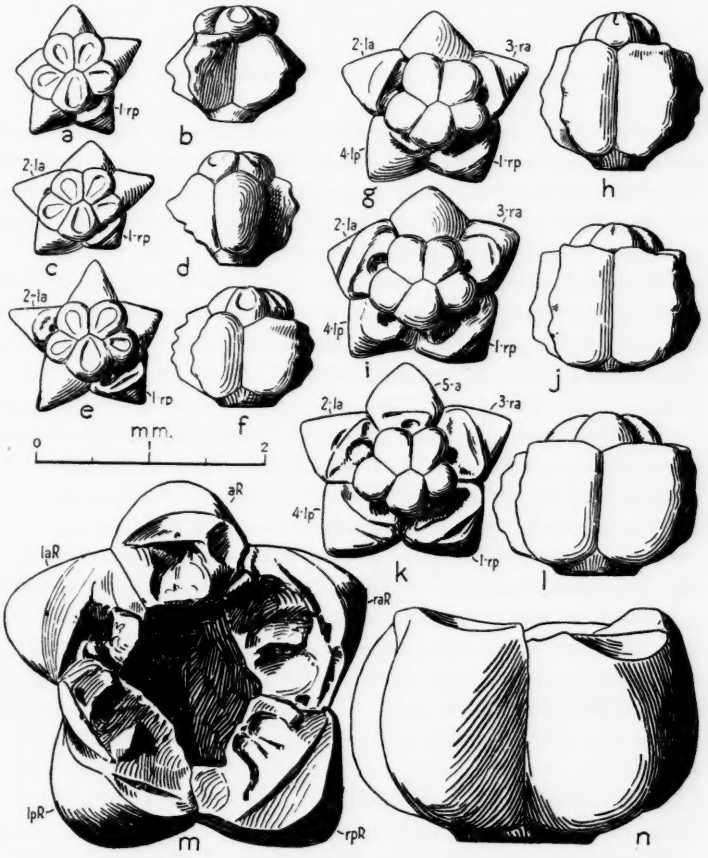

FIG. 13.—Drawings of immature individuals and a mature specimen of *Allagecrinus pecki*, n. sp., from the top of the Cherokee shale about 6 miles northeast of Columbia, Mo. (sec. 27, T. 49 N., R. 12 W.), showing order of development of the arms as indicated by appearance of facets on the radials. Orientation of the immature specimens is determined by identification of the posterior oral plate, which is slightly larger and differently shaped as compared with the others. *a,b*, Ventral and right lateral views of a small calyx having only one arm facet, located on the rpR (paratype Univ. Kansas no. 60791-I). *c,d*, Ventral and left posterior views of another very small specimen having a well developed facet on the rpR and an incipient one on the laR (paratype 60791-H). *e,f*, Ventral and posterior views of a specimen with two well formed arm facets (paratype 60791-D). *g,h*, Ventral and posterior views of a specimen having three well formed facets and a fourth one beginning to appear on the lpR (paratype 60791-A). *i,j*, Ventral and posterior views of a specimen having four distinct arm facets (paratype 60791-B). *k,l*, Ventral and posterior views of a large immature example having distinct facets on all of the RR (paratype 60791-F). *m,n*, Ventral and posterior views of the holotype, which has two facets on the raR and lpR and one facet on the laR, aR, and lpR, making seven facets in all (no. 60791). All drawings to the same scale.

very convex but smoothly rounded, greatest bulge slightly below midheight. The height of the cup is a little less than two thirds of the greatest width. The oral circlet seems not to increase in size appreciably but plates of older specimens appear somewhat smoothly convex instead of hollowed.

The basal circlet is a very low disc without visible sutures between the plates. Almost all of the circlet is covered by the round stem impression, only the distal extremities of the plates lying outside of this area and forming a slope about 0.2 mm in length. The RR of large specimens have fairly evenly rounded form but show a flattened inward-sloping area in the central distal region near the facet. Transverse ridges of the facets are distinct and on their outer slope they bear a small opening for the dorsal canal; the outer ligament area is a shallow crescentic concave space, and the inner part of the facets show well defined broad grooves bordered by longitudinal ridges. The left shoulder of the rpR is beveled slightly so as to form a notch at the junction with the lpR, which rises above the general level of the rpR; an enlargement of the body cavity is seen at the inner edge of the beveled shoulder mentioned. The laR is approximately as wide as the aR, although distinctly narrower than the other plates of this circlet, and its summit is a little lower than those of the adjoining RR. The holotype bears 7 arm facets that are definitely observed and an additional small facet seems to be making appearance on the aR; the distribution of the facets on this specimen (see fig. 13m) is lpR 2, laR 1, aR 1 (?2), raR 2, and rpR 1. A paratype of the same size as the holotype shows the same arrangement of facets except that the aR clearly has 2 facets, one of which is larger than the other. The surface of the cup is smooth.

Measurements of the holotype are: greatest width of cup, 3.5 mm, height of cup, 2.1 mm. Immature examples show a gradual increase in size as indicated in the drawings (fig. 13).

Order of development of arms.—Attention may be called to the evidence furnished by the immature specimens of *A. pecki* as to the order of appearance of arms in different rays. This is

indicated by the successive development of facets at the summit of the RR. The number of specimens that are available for study is not large enough to demonstrate that the order here indicated holds rigorously, but no deviations from it are seen in these specimens. The first ray to show an arm facet is the rpR (fig. 13a, c) and next is the laR (fig. 13c, e); seemingly the raR precedes the lpR, and last of all comes tha aR as a facet-bearing plate. Although first to develop arm appendages, the rpR and laR remain one-armed, whereas the other RR may become multi-armed.

Comparison of the order of appearance of facets observed in *A. pecki* with that reported in other microcrinoids is interesting. Investigations of some forms indicate that a certain pair of facets develops a little earlier than another pair, or three of the facets may be recognized as belonging to the first arm-bearing immature stage that is discriminated. In these it is not possible to determine an order of precession that takes account of every ray. The following summary of the results of studies indicates by bracketed combinations the two or more radials whose order with respect to themselves is undetermined; the order *within* these combinations as given in the table is arbitrary.

Order of development of arm facets on different rays of microcrinoids

SPECIES	FIRST	SECOND	THIRD	FOURTH	FIFTH
Allagecrinus pecki, n. sp.	rpR	laR	raR	lpR	aR
Allagecrinus austinii[1]	rpR	laR	raR	lpR	aR
Hybochilocrinus americanus[2]	rpR	laR	raR	lpR	aR
Hybochilocrinus rowleyi[3]	rpR	laR	raR	lpR	aR
Trophocrinus corpulentus[4]	rpR	laR	lpR	—	—
Callimorphocrinus pristinus[5]	rpR	laR	raR	lpR	aR
Callimorphocrinus scoticus[6]	Variable				

[1] Wright (1933, p. 203). [2] Peck (1935, p. 768). [3] Peck (1936, p. 285). [4] Peck (1936, p. 287). [5] Peck (1936, p. 287). [6] Wright (1932, p. 357).

The data presented are not conclusive but they strongly suggest that this ontogenetic character is significant in taxonomic studies.

Remarks.—The distinguishing specific character of *Allagecrinus pecki* seem to be found chiefly in the shape of the cup, its smooth surface, and possibly its small size. The species corresponds to *A. strimplei* in the distribution of arm facets and the lack of surface markings, but it is considerably smaller and proportionally much taller. *A. strimplei* and *A. bassleri* occur in beds of the Missouri stage, which belong several hundred feet above the horizon containing *A. pecki.*

Occurrence.—Topmost part of the Cherokee shale, immediately underlying the Fort Scott limestone, Des Moines stage (lower Pennsylvanian); the holotype and all paratypes except two are from R. E. Peck's loc. 671, south of Hinkson Creek in SE Sec. 27, T. 49 N., R. 12 W., Boone County, Missouri; two paratypes are from Peck's loc. 674, SW Sec. 34, T. 49 N., R. 12 W., Boone County, Missouri.

Types.—Holotype, Kansas Univ. no. 60791, paratypes nos. 60791A–J, from loc. 671; and paratypes nos. 60801, 60801A, from loc. 674. Types deposited in the University of Missouri.

Allagecrinus sp., cf. *A. bassleri* Strimple

Plate II, figures 7a–c; text figures 12i–l

A single dorsal cup of unusually large size belonging to a species of *Allagecrinus* is here figured and described briefly, for the reasons that it constitutes a new record of the stratigraphic occurrence of the genus and that it illustrates with special clearness various structural features. The specimen is larger than most of the examples of *Allocatillocrinus rotundus* that have been found, and comparison of the form of homologous features is instructive. The large *Allagecrinus* comes from the Wewoka formation, near Okmulgee, Okla.

The cup is broad and low, the height being only a little more than one third of the greatest width; the base is flat except for the gentle concavity of the stem area, which is also greater than one third of the width. Only the tips of the BB are visible around the stem impression. The RR are evenly bulbous but they are unequal in size, the lpR being the largest. The summit areas make a broad inward sloping platform that is subdivided

by the longitudinal ridges between the facets. The distribution of the facets (lpR 5, laR 1, aR 3, raR 3, rpR 1) and the shape of the cup correspond so closely to these features in typical examples of *Allagecrinus bassleri* Strimple that the specimen under discussion might be referred to this species except for a few considerations. The distinctions may be unimportant, and if additional specimens of the large form support identification as *A. bassleri* the range of this upper Missouri allagecrinid will be greatly extended downward. The Wewoka specimen, which measures 8.8 mm across the widest part, is approximately twice as large as average cups of *A. bassleri*, although it is not so much greater than the largest reported example of that species (diameter 6 mm). The surface of the Wewoka specimen seemingly lacks any decoration, whereas *A. bassleri* is beautifully marked by fine granulation.

Occurrence.—Wewoka formation, upper Des Moines stage, lower Pennsylvanian; below dam at reservoir about 6 miles southwest of Okmulgee, Okla.

Figured specimen, Kansas University no. 60531, collected by Ben Taylor, University of Tulsa.

Genus ALLOCATILLOCRINUS Wanner, 1937

Allocatillocrinus rotundus, n. sp.

Plate II, figure 8; plate III, figure 1; text figures 6a–w, 14a–f

Dorsal cup of mature specimens bowl-shaped, sub-hemispherical, height about one half greatest width; the cups of immature examples distinctly lobate.

Basal circlet very low, pentagonal in outline, largely covered by the proximal stem segment, distal portion sloping upward and confluent with the RR. Three unequal plates are visible in some specimens, the small one in the posterior interradius; commonly the sutures between BB are not apparent and the plates may be fused.

RR unequal, consisting of three relatively large plates, the lpR, aR and raR, and two smaller ones, the laR and rpR; proximal edges of RR almost exactly equal in length, but at the distal

margin the lpR is distinctly wider than the aR and raR, and all of these greatly exceed the laR and rpR. The suture between the posterior RR is straight, but the others curve strongly, the aR considerably overlapping the edges of the adjoining plates and the raR and lpR also projecting strongly toward the left at the upper margin. The laR and rpR are shorter than the other plates, so that there are distinct notches at the top of the cup in the position of these plates. The single arm facet borne by the laR and rpR is two or three times as wide as the arm facets on the other RR. The first arm segment is attached to the laR in a few specimens, filling the space above the laR facet between the lpR and aR and projecting about 1 mm above the level of the summits of these plates. The arm is massive, its thickness about equal to its width. The exterior surface is rounded, the sides flattened, and the inner side bears a very narrow groove; the articular surface at the top of the brachial is smooth. It is noticeable that the facet at the anterior extremity of the raR is also larger than the other facets.

Tabulation of the number and distribution of the arms, as revealed by position of the facets, is indicated below, with notation of the diameter of the cup. Specimens having a diameter of less than 4.5 mm have the characters of *Allagecrinus*, as discussed elsewhere in this paper.

FIG. 14.—Camera lucida drawings of dorsal cups of *Allocatillocrinus*.

a–f, *Allocatillocrinus rotundus*, n. sp., from the Brentwood limestone of northeastern Oklahoma. *a,b*, Ventral and side views of a large paratype (Univ. Kansas no. 451928B), with lpR toward the observer; from Keough quarry, 2 miles north of Fort Gibson, Okla., collected by Arthur L. Bowsher. *c,d*, Ventral and side views of the holotype specimen (Univ. Kansas no. 451928A), a very large and unusually well preserved example having a relatively small number of facets on the lpR; from Keough quarry, collected by Ralph H. King. *e,f*, A mature but small paratype (Univ. Kansas no. 73851D) from Greenleaf Lake, southeast of Bragg, Okla.

g–j, *Allocatillocrinus rotundus multibrachiatus*, n. subsp., from the Brentwood limestone. *g,h*, Articular surface of the lpR and side view of a paratype (Univ. Kansas no. 73852A), from Greenleaf Lake, Okla., collected by Arthur L. Bowsher. *i,j*, Ventral and side views of the holotype, (Univ. Kansas no. 451929A), from Keough quarry, collected by L. R. Laudon. All figures × 5.

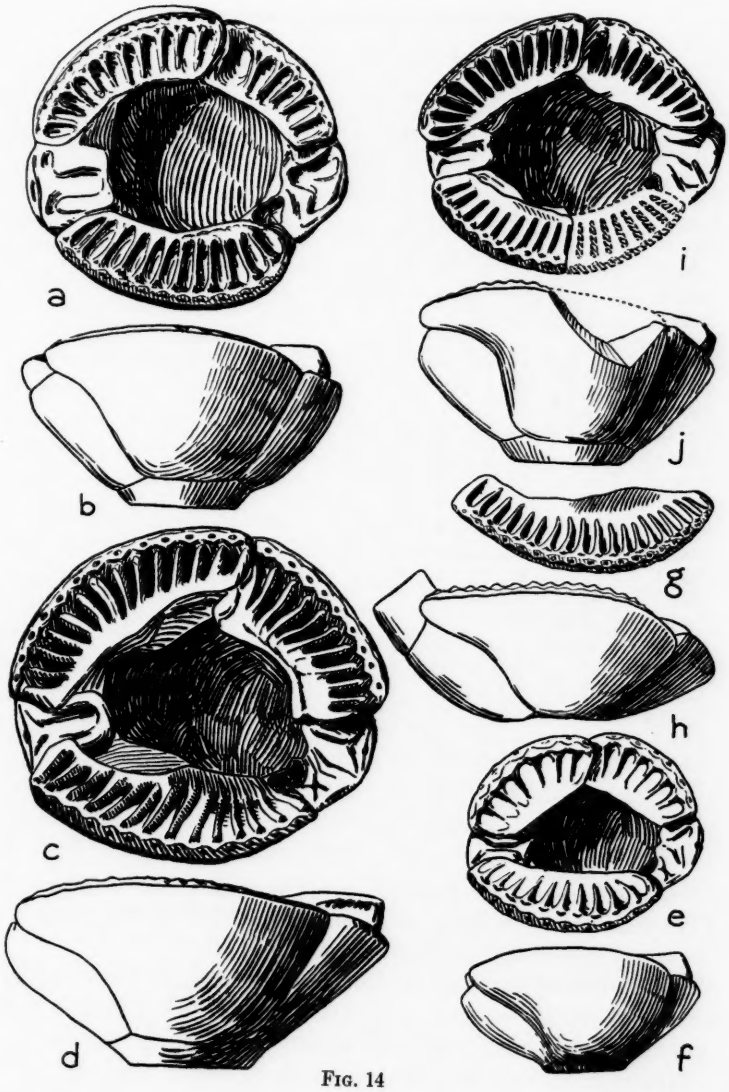

FIG. 14

Measurements of Allocatillocrinus rotundus, n. sp.

SPECIMEN	AV. FACETS 10 MM.	NUMBER OF ARM FACETS					DIAMETER IN MM.	REMARKS
		lpR	laR	aR	raR	rpR		
451928B	16.0	16	1	14	10	1	11.7	Smoothly rounded
*451928	13.0	13	1	13	9	1	11.0	" "
451928A	13.4	12	1	11	6	1	10.0	" "
73851C	16.4	13	1	10	7	1	7.5	Faintly lobed
73851AA	13.0	12	1	9	8	1	9.8	" "
73851U	14.0	13	1	9	8	1	8.2	" "
73851Z		12	1	9	7	1	7.5	" "
73851W		11	1	9	7	1	7.2	" "
73851N	13.0	11	1	?8	7	1	8.0	" "
73851AB	16.0	11	1	8	6	1	6.5	Lobate
73851V	16.0	10	1	8	6	1	6.2	"
73851R	16.0	11	1	7	7	1	6.5	"
73851D	14.0	11	1	7	6	1	6.8	"
73851K	16.5	10	1	7	6	1	6.5	"
73851AC		9	1	7	6	1	6.0	"
73851H	16.2	9	1	7	5	1	6.0	Strongly lobate
73851J	16.1	10	1	6	5	1	5.7	" "
73851B	16.2	9	1	6	6	1	5.3	" "
73851F	16.0	8	1	6	6	1	5.1	Lobate
73851I		8	1	6	6	1	5.0	Strongly lobate
73851S	14.5	8	1	5	7	1	6.0	" "
73851G	16.4	8	1	5	5	1	5.1	" "
73851AD	17.0	8	1	5	5	1	4.8	" "
73851Y		7	1	5	5	1	4.8	" "
73851E	15.5	7	1	4	4	1	4.1	" "
73851A		6	1	4	4	1	3.9	" "
73851L		5	1	3	3	1	3.3	" " , nodose
73851M		4	1	3	3	1	3.2	" " , "
73851O		3	1	2	2	1	2.3	" " , "
73851P		2	1	1	2	1	2.0	" " , "

* Holotype.

For comparison, the distribution of the arms in the holotype of *A. rotundus* and specimens of *A. morrowensis*, *A. scoticus*, and *A. carpenteri* is indicated in the table on page 131.

The surface of the cup, in younger specimens, is decorated by somewhat widely spaced very low but distinct granules and tubercles, but in adult stages the surface of the cup is smooth.

Measurements of the holotype specimen and a very well preserved paratype (no. 451928A), in millimeters, are respectively

Arms in Species of Allocatillocrinus

(Figures in italics indicate percent of the total number of arms)

SPECIES	TOTAL ARMS	lpR	lnR	aR	raR	rpR
A. rotundus, n. sp., holotype	37	13	1	13	9	1
	100	*35*	*2.7*	*35*	*24*	*2.7*
A. morrowensis (Strimple)	38	9	1	15	12	1
	100	*24*	*2.5*	*39.5*	*31.5*	*2.5*
A. scoticus (Wright)	30	9	1	12	7	1
	100	*30*	*3.3*	*40*	*23*	*3.3*
A. carpenteri (Wachsmuth)	24	8	1	9	5	1
	100	*33*	*4.2*	*37.5*	*21*	*4.2*

as follows: height of cup, 5.7 and 5.5; greatest width of cup, 11.0 and 10.0; width of basal circlet, 5.5 and 5.0; diameter of stem impression, 4.1 and 3.5.

Remarks.—The shape of the dorsal cup distinguishes *A. rotundus* from any of the described species of this genus, for *A. carpenteri* and *A. scoticus* have more or less steeply conical form with straight sides, and *A. morrowensis* is distinguished by the strongly tumid plates which give a subpentagonal or subtrigonal aspect to the cup. Distinguishing features are also found in the number and distribution of the arms as shown in the foregoing tabulation.

Occurrence.—Brentwood limestone, Morrow stage, lower Pennsylvanian; Kansas University loc. 4519, near Keough quarry about 2 miles north of Fort Gibson, Okla., in sec. 36, T. 16 N., R. 19 E.; loc. 7385, spillway below Greenleaf reservoir, southeast of Braggs, Okla., near center sec. 10, T. 13 N., R. 20 E. Most of the specimens were obtained from the latter place, being washed from shaly beds near the base of the exposure; the thickness of strata containing the fossils is about 2 feet and the width of the exposure about 30 feet.

Types.—Holotype, Kansas University no. 451928, from loc. 4519, collected by Ralph H. King. Paratypes, nos. 451928A, B and some 30 specimens from loc. 7385, collected by L. R. Laudon, A. L. Bowsher, and R. C. Moore. Types distributed to U. S.

National Museum (holotype and some paratypes), University of Kansas, University of Tulsa.

Allocatillocrinus rotundus multibrachiatus, n. subsp.

Plate III, figures 2, 3; text figures 14e–j

A few of the dorsal cups of the *Allocatillocrinus rotundus* type that are found both at the Fort Gibson and Greenleaf Lake localities in eastern Oklahoma, differ in the distinctly closer spacing of the arm facets on the large radials. Also, two of these cups, though not especially large, have 18 facets on the lpR, which is 6 or 7 more than on specimens of similar size that are referred to *A. rotundus*. These cups are differentiated as a subspecies, called *multibrachiatus*. In characters except the facets there seem to be no grounds for distinction of this form from *A. rotundus*.

The holotype has 18 facets on the lpR, 12 on the aR and 9 on the raR; a paratype has 18, 10, and 8 facets on these plates, respectively, and another paratype shows ?16, ?9, and 8 facets. The holotype has a greatest width of 9.0 mm and a height of 4.8 mm.

Occurrence.—Same as *Allocatillocrinus rotundus*.

Types.—Holotype, Kansas University no. 451929, from loc. 4519, north of Fort Gibson, collected by L. R. Laudon; paratype no. 451929A, from same locality. Paratype no. 73852, from loc. 7385 at Greenleaf Lake, collected by A. L. Bowsher. Types deposited in the U. S. National Museum.

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EXPLANATION OF PLATE II

Allagecrinus constellatus, n. sp., from the Oologah limestone at Garnett quarry, 7 miles northeast of Tulsa, Okla; × 5.5.

1.—Paratype, no. 458912C, a medium-sized specimen showing pear-shaped radial plates; *a*, dorsal view; *b*, ventral view.

2.—Paratype, no. 458912D, a young specimen with strongly stellate outline and relatively coarse ornamentation; *a*, dorsal view, *b*, ventral view.

3.—Paratype, no. 458912E, a young specimen; *a*, dorsal view; *b*, ventral view.

4.—Holotype, no. 458912A, the largest observed example having bluntly rounded radials, the outer part of the anterior radial broken; *a*, dorsal view; *b*, ventral view.

Allagecrinus dignatus, n. sp., from the Oologah limestone, at Garnett quarry, 7 miles northeast of Tulsa, Okla. × 5.

5.—Paratype, no. 458911N, a perfectly preserved specimen of average size; *a*, dorsal view; *b*, ventral view.

6.—Holotype, no. 458911A, a robust specimen; *a*, dorsal view; *b*, ventral view.

Allagecrinus sp., cf. *A. bassleri* Strimple, from the Wewoka formation, at dam 6 miles southwest of Okmulgee, Okla.; × 5.1.

7.—Figured specimen, no. 60531A, a large, well preserved dorsal cup, *a–c*, dorsal, posterior and ventral views.

Allocatillocrinus rotundus, n. sp., from the Brentwood limestone, at Keough quarry, 2 miles north of Fort Gibson, Okla.

8.—Paratype, no. 451928B, collected by Arthur L. Bowsher, a very well preserved large specimen showing relatively coarse spacing of arm facets; *a*, dorsal view × 4.9; *b*, posterior view, showing the straight suture between the lpR and rpR, × 4.9; *c*, central view, × 5.2; *d*, view from the side of the laR, showing the low position of the summit of this plate and the strongly overlapping edges of the aR and lpR × 4.9; *e*, view of the raR and aR, × 4.9.

EXPLANATION OF PLATE III

Allocatillocrinus rotundus, n. sp., from the Brentwood limestone, Morrow stage, lower Pennsylvanian, near Keough quarry, 2 miles north of Fort Gibson, Okla.

1.—Holotype, no. 451912, a perfect dorsal cup that has nearly the maximum observed size; *a*, posterior view, showing the depressed position of the summit of the rpR, × 6.2; *b*, ventral view, × 6.2; *c*, dorsal view, × 5.5.

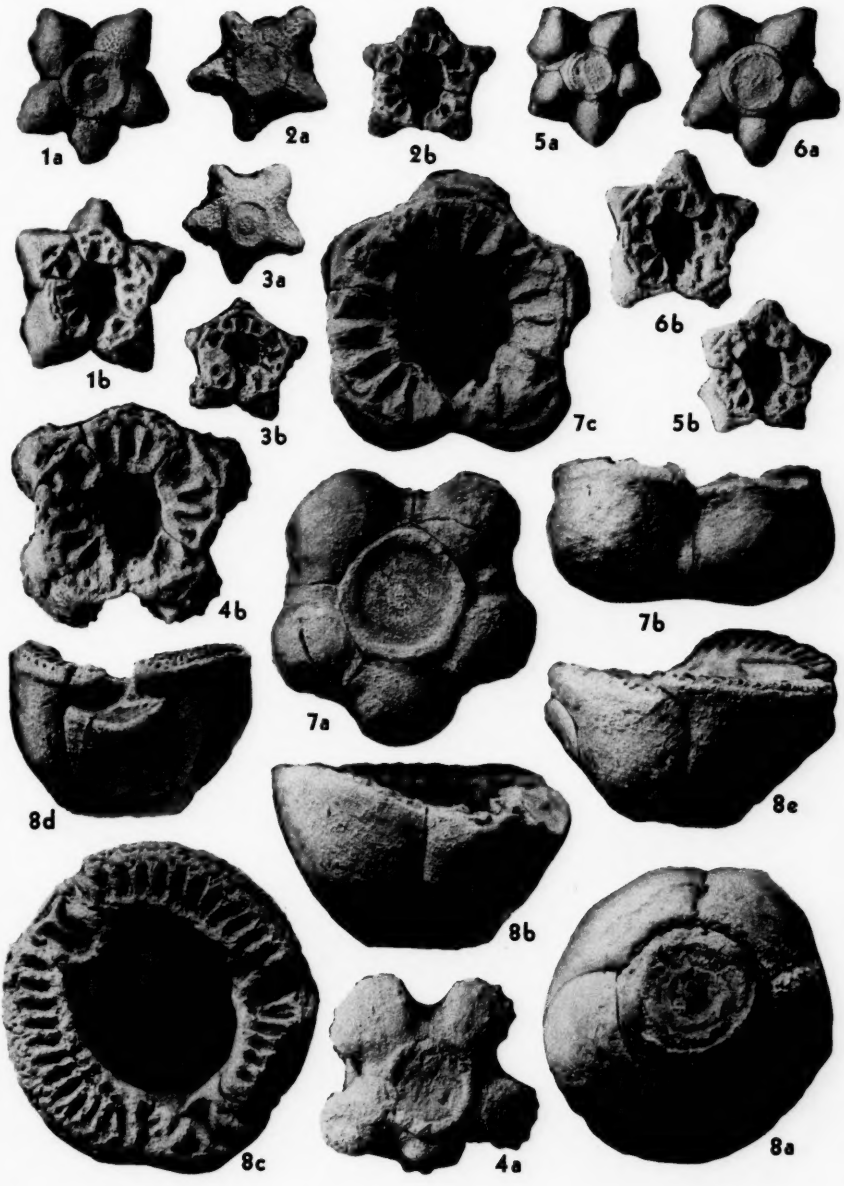
Allocatillocrinus rotundus multibrachiatus, n. subsp., from the Brentwood limestone, Morrow stage, lower Pennsylvanian, eastern Oklahoma.

2.—Holotype, no. 451929, from near Keough quarry, 2 miles north of Fort Gibson, a nearly perfect dorsal cup; *a*, posterior view, × 6.2; *b*, ventral view, showing the closely spaced facets, × 6.2.

3.—Paratype, no. 73852, from Greenleaf Lake, southeast of Braggs, Okla., a laterally compressed dorsal cup having the typical characters of the subspecies; the lpR, on the left side of the photograph, bears 18 facets; just above it, the projecting upper articular surface of the first brachial of the laR may be seen, this arm being several times larger than those attached to the large radials, × 6.2.

Allagecrinus constellatus, n. sp., from the Oologah limestone at Garnett quarry, 7 miles northeast of Tulsa, Okla., × 6.2.

4.—Paratype no. 458912B, a nearly perfect dorsal cup slightly smaller than the holotype, showing the bluntly rounded lobed appearance of the radials; *a*, ventral view; *b*, dorsal view.


1a
2a
2b
5a
6a
1b
3a
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8c
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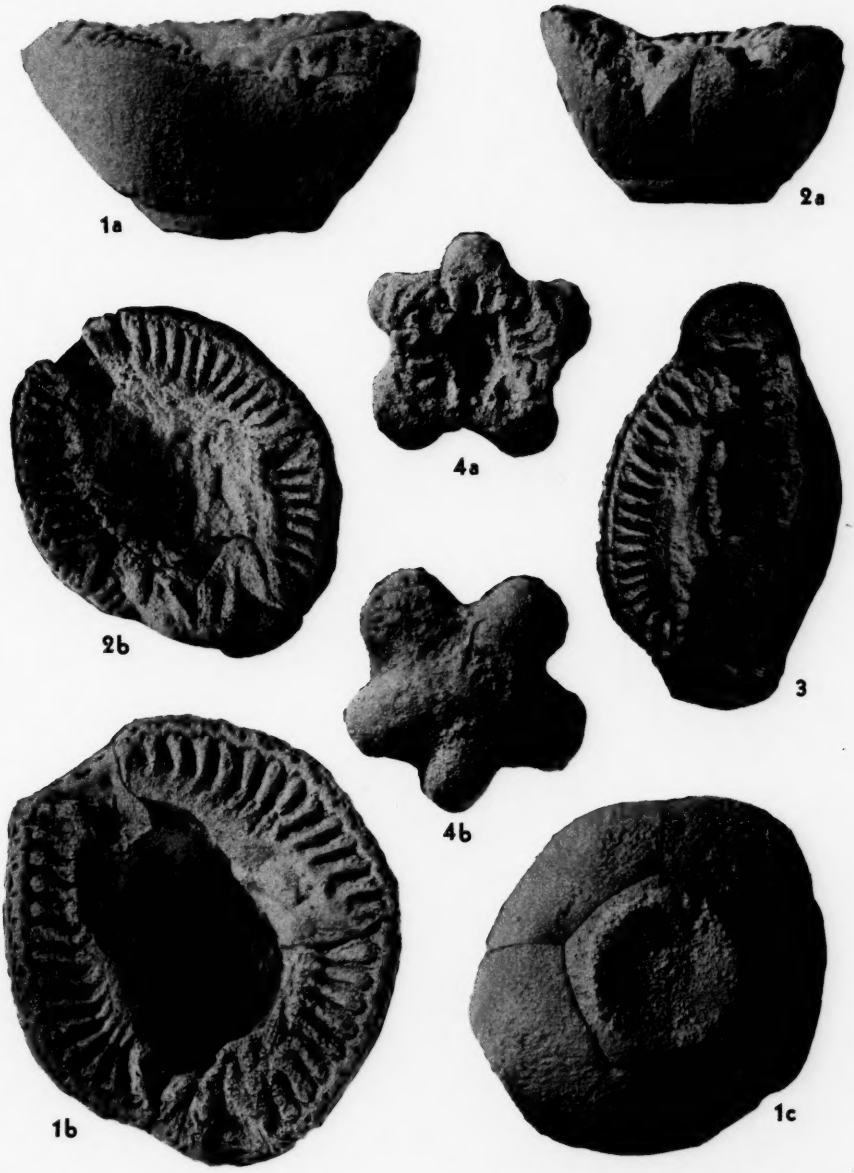
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